UNIVERSITÉ DU QUÉBEC À CHICOUTIMI

# ANALYSE DU RÔLE DES COMPOSANTES DE LA DIVERSITÉ SUR LE FONCTIONNEMENT DES ÉCOSYSTÈMES MARINS BENTHIQUES INTERTIDAUX

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN BIOLOGIE

PAR

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SEPTEMBRE 2015

À MA FAMILLE

# RÉSUMÉ

Les changements climatiques et une forte utilisation des habitats par l'Homme sont à l'origine de nombreux bouleversements environnementaux. Ces perturbations provoquent une perte de la biodiversité. Plusieurs travaux de recherches ont démontré un impact négatif de la perte de biodiversité sur le fonctionnement des écosystèmes et par conséquent, sur les services rendus à l'Homme par la biodiversité (c.-à-d. pêcherie, agriculture, dépollution de l'eau et air, capture de $CO_2$, etc.). L'étude du fonctionnement des écosystèmes et l'importance de la diversité dans le maintien des processus écologiques revêtent d'une toute nouvelle importance. La zone benthique intertidale possède une diversité appréciable, est facile d'accès et les espèces vivantes y sont facilement manipulables. Selon les scénarios actuels d'Ouranos et du GIEC, des bouleversements majeurs d'origines anthropologiques vont y provoquer une disparition des glaces de mers, à une augmentation du niveau et de la température de l'eau ainsi qu'une forte érosion des berges dans les prochaines décennies. Tous ces changements vont avoir un impact sur la dynamique et la structure des communautés benthiques intertidales. Pourtant, le fonctionnement de ces communautés reste encore peu connu. Ce projet de recherche tente d'approfondir les relations entre le fonctionnement (stabilité, établissement et productivité) des communautés benthiques intertidales et les facteurs de richesse, d'abondance (équitabilité, dominance) et d'identité des espèces. Pour ce faire, trois études ont été élaborées. La première étude porte sur le rôle de la richesse et de l'équitabilité sur la stabilité temporelle des communautés benthiques : suivi sur 2 ans des communautés naturelles. La seconde étude porte sur l'impact d'un changement de richesse, d'équitabilité, d'identité et d'abondance des espèces fondatrices (tel que macroalgues et moules) sur l'établissement des communautés associées et leur productivité : expérience *in situ* avec manipulation des communautés. La troisième étude veut mettre en évidence le rôle de la richesse, de l'équitabilité, de l'identité et de l'abondance des macroalgues sur la productivité primaire (production primaire nette, respiration et production primaire brute), étude en mésocosme. Contrairement à ce qui était attendu, les résultats de ces études démontrent que la richesse et l'équitabilité n'ont qu'un impact positif limité sur la stabilité et l'établissement des communautés benthiques. Cet impact semble être masqué par les conditions environnementales. La richesse, l'équitabilité, l'identité et l'abondance des espèces fondatrices ne semblent pas affecter la diversité des espèces associées qui colonisent le milieu, toutefois leur structure est affectée par un changement de diversité. Toutefois, la richesse, l'identité et l'abondance ont un effet positif sur la productivité primaire. Généralement, l'équitabilité a un effet positif sur la productivité bien que parfois, l'effet soit négatif. L'équitabilité semble avoir un effet indirect sur la productivité en atténuant l'effet de richesse. Mon projet de recherche a permis d'avoir plus de précision sur le lien entre chacune des composantes de la biodiversité sur le fonctionnement des communautés benthiques.

Mots clés : diversité, fonctionnement des écosystèmes, équitabilité, productivité, stabilité

# ABSTRACT

Climate change and stress on habitats induce by Human are responsible for environmental upheavals. Those disturbances cause a lost in biodiversity. Many studies demonstrate a negative impact of biodiversity lost on ecosystem functioning with consequences on the human services provided by the biodiversity (fisheries, agriculture, water filtration, $CO_2$ capture etc). The study of community dynamics and the role of diversity in maintaining ecological processes are now more important than ever. Marine ecosystem, and more precisely benthic intertidal zone is perfect to study the le relationship between diversity and ecosystem functioning. This zone has level of diversity not negligible, easy to access and organisms are easy to manipulate. GIEC scenarios predict major changes in all ecosystems worldwide and the intertidal zone will not be at rest. Ice will tend to disappears, temperature and sea level will rise and salinity will be much more variable. Those changes will have a negative impact on benthic community structure and dynamic. Nonetheless, benthic ecosystem functioning remain unclear and further studies must be done to really understand the consequence of a change in biodiversity on the dynamic of those communities. This research aim to define the relationship between the functioning (stability, establishment and productivity) of the benthic intertidal community and diversity variables, the richness, evenness, identity and abundance of species. To do so, 3 studies were elaborated. The first study aim to define the role of richness and evenness on community stability, without manipulation, two years data set. The second one aim to understand the impact of a change in richness, evenness identity and abundance of habitat forming species on species establishment and community productivity. This study is *in situ,* with manipulation of the habitat forming species. The last study is in mesocosme and aim to define the role of richness, evenness identity and abundance of the main macroalgae present on the shores on community primary productivity. Contrary to the hypothesis, the results show that richness and evenness has a limiting positive impact on community stability and establishment. This impact seems to be damp by the abiotics factors on the field. Nonetheless, richness, abundance and identity all have a positive impact on primary productivity. At high evenness, richness effect is more present than at low evenness. This theses will help to better anticipates the consequences of a change in biodiversity on benthic ecosystem functioning and will give better tools to the politics managers to help them take better decision regarding the ecosystem management.

Key words: diversity, ecosystems functioning, evenness, productivity, stability

# AVANT PROPOS

Il y a de ça 6 ans maintenant, je reçus un courriel me disant que ma candidature est retenue pour le projet de recherche portant sur la dynamique des communautés benthiques. Sortant tout droit d'une maitrise en foresterie, j'étais paniquée à l'idée de ne rien connaître sur ce sujet et d'avoir un directeur assez fou pour prendre une forestière pour travailler en aquatique. J'étais surtout incroyablement heureuse de pouvoir enfin vivre mon rêve de toujours, devenir biologiste en milieu marin. Maintenant que je regarde ce que j'ai accompli depuis que j'ai commencé, je me rends compte de la chance que j'ai eue de pouvoir vivre cette expérience qui m'a beaucoup enrichie en tant que scientifique, mais aussi en tant que personne. Toutes ces émotions m'ont fait grandir et ont fait de moi la biologiste que je suis aujourd'hui. Le moment où mon premier article a été accepté pour publication restera pour toujours gravé dans ma mémoire comme un des plus beaux moments de ma vie.

Bien sûr, je n'aurais jamais pu réussir ce doctorat sans le support de mes parents, mon frère, mes tantes, mes oncles et mes cousins, cousines que j'aime de tout mon cœur et de mes amis qui me manquent tant. J'entendais mes amies, Catherine, Soraya, Anna, Winna et mon futur époux Francis me dire « T'es la meilleure, ne lâche pas ma belle, tu vas y arriver » ainsi que mes parents et mon parrain me dire: « Tu as travaillé assez fort, tu es capable de continuer et tu vas l'avoir». Cette thèse est mon rêve et le fruit de dur labeur, mais j'ai toujours été capable de passer au travers des obstacles et des moments difficiles grâce à leur support et leur amour.

Mes collègues et amis dans le laboratoire sont devenus une source de réconfort au travail. Merci à Anne-Lise Fortin et Angélique Lazartigues qui m'ont donné un tas de conseils tout au long de mon doctorat. Merci à tous ceux qui sont venus avec moi sur terrain, les résultats de mes travaux je les dois également à vos efforts et votre capacité de travailler dans des conditions climatiques parfois plus qu'extrêmes, Pierre Corbeille-Carier, Laetitia Joseph, Winna H. Landry, Stéphanie Cimon, Vanessa Paradis, David-Alexandre Gauthier, Steeve Lavoie, Hélène Perelman et Sonya Lévesque. Un merci tout spécial à Mérilie Gagnon qui a été la toute première à venir avec moi sur le terrain et qui possédait déjà la science infuse et me l'a transmise. Les moments passés avec vous sont pour moi des souvenirs précieux et je

ne vous oublierai pas. Merci à Dominique Davoult et son équipe de m'avoir accueillie pour mon stage à la station biologique de Roscoff. Merci à Ladd E. Johnson et Chris McKindsey pour, le prêt de matériel et les très bons commentaires et conseils sur mes travaux. Merci aux membres laboratoire des sciences aquatiques de m'avoir aussi bien accueillie. Ils ont su me faire sentir comme chez moi et nous avons eu bien du plaisir durant ces années. J'ai de très beaux souvenirs de vous tous que je garderai toujours précieusement. Je garde celui qui m'a le plus poussée, aidée et inspirée dans mes travaux pour la fin, car tout le monde le sait, le meilleur est pour la fin. Je remercie donc chaleureusement mon directeur Mathieu Cusson qui m'a formée et encouragée. Ses conseils ont toujours été extrêmement utiles, constructifs et très appréciés. Il m'a transmis son savoir, sa curiosité et son enthousiasme pour le milieu benthique et c'est cette même curiosité qui m'a animée durant tout mon doctorat et m'a poussée à toujours voir plus loin et chercher les réponses. J'ai dû lui causer bien des maux de tête...et réciproquement, mais je lui serai toujours reconnaissante de la chance qu'il m'a donnée de pouvoir poursuivre ma passion et d'avoir fait de moi une biologiste en milieu marin.

Bien sûr aucune recherche n'est possible sans soutien financier, je remercie donc Québec-Océan, le Fonds de recherche du Québec – Nature et technologies (FRQNT) Programme Établissement de nouveaux chercheurs universitaires et Conseil de recherches en sciences naturelles et en génie du Canada CRSNG pour leur soutien financier.

Je termine ces remerciements sur les paroles d'Hubert Reeves remplis de sagesse qui s'appliquent très bien à cette thèse :

Devenir adulte, c'est apprendre à vivre dans le doute et à développer, au travers des expériences, sa propre philosophie, sa propre morale. Éviter le "prêt-à-penser".

Il sera ici question de science, ce qui n'exclut pas la poésie.

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# CHAPITRE 1 : INTRODUCTION GÉNÉRALE

## MISE EN CONTEXTE DE MON PROJET DE THÈSE

Les changements climatiques d'origine anthropique tels que pollution de l'air, l'exploitation abusive des ressources et une diminution de la superficie et de la qualité des habitats sont les causes premières de la perte accélérée de la biodiversité. Naeem et coll. (1994a) ont démontré qu'une perte de la biodiversité couplée à une perte des ressources génétiques engendre une diminution de la productivité et de la capacité de tampon des écosystèmes contre les perturbations et peuvent altérer les services rendus à l'Homme par la biodiversité. Cette réalité a donné un nouvel essor à l'étude de la relation entre la biodiversité et le fonctionnement des écosystèmes (Cottingham et al. 2001) tels que le recyclage des nutriments, la décomposition et la photosynthèse. Toutefois, la majorité des études portant sur ce sujet ont été réalisées en milieu terrestre. Les études portant sur lien entre la diversité et le fonctionnement des écosystèmes sont principalement réalisées en mésocosme et bien souvent sur des communautés d'organismes unicellulaire (Crowe et al. 2012). D'autres études en milieu naturel sont nécessaires afin de bien comprendre tous les aspects et la dynamique des milieux marins.

Dans la littérature, les conclusions des recherches divergent. En effet, plusieurs recherches démontrent un effet positif de la diversité sur le fonctionnement des communautés telle que la productivité (Tilman 1996, McGrady-Steed 1997, Hector et al. 1999) alors que d'autres trouvent un effet négatif (Dunstan and Johnson 2004, Valdivia and Molis 2009) ou ne trouvent aucun impact (Wardle 1999). De par la divergence et le manques de consensus, notre connaissance du milieu marin est très limitée et il y a un besoin pour des travaux empiriques de terrain dans ce milieu (Widdicombe and Somerfield 2012).

Dans cette thèse, j'ai évalué trois fonctions de l'écosystème qu'une perte de la diversité pourrait affecter soit la stabilité, la facilitation et la production primaire. Ces fonctions seront contrastées avec la richesse, l'équitabilité, l'identité et l'abondance des espèces. Le site à l'étude est situé dans la zone intertidale rocheuse de l'estuaire

du Saint-Laurent. Il est considéré comme en milieu subarctique de par la température de l'eau dépassant rarement les 12 degrés Celsius en été.

## OBJECTIFS, HYPOTHÈSES, RÉSUMÉ DES MÉTHODES ET LIEN ENTRE LES TROIS ARTICLES

Ma thèse comporte 3 volets (articles) ayant un objectif commun de mieux comprendre le rôle de la richesse, de l'équitabilité de l'identité et de l'abondance des espèces sur le fonctionnement des communautés benthiques. Toutefois, chaque volet a ses objectifs spécifiques et traitera un aspect différent du fonctionnement des écosystèmes. Dans la littérature, la diversité a souvent été mesurée en termes de richesse uniquement et l'équitabilité est un paramètre qui a été négligé. Ce dernier mesure la répartition des abondances entre les espèces et est un aspect nouveau qui a été démontré comme ayant un effet différent de la richesse sur la dynamique des communautés. De plus, il a été suggéré qu'un changement dans la répartition des abondances (équitabilité) va se réaliser avant qu'une perte de richesse se produise au sein des communautés (Hillebrand et al. 2008). Toutefois le rôle de l'équitabilité à l'intérieur des communautés est encore peu connu, c'est pourquoi un intérêt particulier y sera accordé dans chaque volet.

Le premier article (volet 1) a pour objectif de mieux définir le rôle de la richesse et de l'équitabilité sur la stabilité temporelle des abondances des communautés benthiques. L'hypothèse émise est qu'une plus grande richesse et équitabilité va augmenter la stabilité et la productivité des communautés. Pour ce faire, j'ai effectué un suivi des communautés naturelles (aucune manipulation n'a été apportée aux communautés) sur 2 sites, 2 ans dans 40 quadrats avec 2 niveaux d'équitabilité. Cette partie permet de connaitre la variation naturelle des abondances d'espèces.

Le second article (volet 2) porte sur l'impact d'un changement de richesse, d'équitabilité, d'identité et d'abondance des espèces fondatrices, telles que les macroalgues et les moules, sur l'établissement d'espèces associées et la production

primaire de la communauté. Comme chaque espèce fondatrice possède des caractéristiques qui lui sont propres, un changement d'identité devrait modifier la composition des espèces associées. De même, une augmentation de la richesse, de l'équitabilité et de l'abondance devrait favoriser l'établissement d'organismes et ainsi accroître la diversité. Pour tester ces hypothèses, j'ai manipulé *in situ* la richesse, l'équitabilité, l'identité et l'abondance des espèces fondatrices dans des assemblages artificiels sur le milieu intertidal. La durée de colonisation par les espèces associées a été de 4 mois soit de mai à la fin d'aout 2011. La productivité a été mesurée au mois de juillet où le maximum de la production des algues est atteint.

Le troisième article (volet 3) porte sur le rôle de la richesse, de l'équitabilité, de l'identité et de l'abondance des macroalgues sur la productivité primaire. Une augmentation de la richesse, de l'équitabilité et de l'abondance devrait augmenter la productivité primaire et même mener à un effet d' « overyielding ». Ces hypothèses ont été testées en mésocosmes. Les principales espèces d'algues de canopée et de sous canopée ont été récoltées dans le milieu intertidal, à proximité de la zone d'expérimentation des deux autres volets. Les assemblages reflétant des communautés naturelles d'algues ont été montés avec divers niveaux de richesse et d'équitabilité souhaités et la production primaire a été mesurée.

Le volet 1 fournit de l'information sur la variabilité naturelle des communautés benthiques. Cette variabilité a été contrastée avec les niveaux de richesse et d'équitabilité naturelles afin comprendre la dynamique des communautés avant d'effectuer des manipulations aux volets 2 et 3. Dans le volet 2, les communautés ont été manipulées *in situ* nous permettant d'avoir un équilibre entre la dynamique naturelle des communautés et l'expérimental en mésocosme. En manipulant les variables (richesse) sur le terrain, il a été possible de mieux cerner la réponse des communautés associées d'espèces face à un changement dans les composantes de la diversité (richesse, équitabilité, identité et abondance) des espèces fondatrices identifiées lors du volet 1. Le volet trois étant en mésocosmes, permet de contrôler les

biomasses et d'affiner la réponse ds composantes de la diversité des communautés sur la production primaire. On passe donc du volet 1 où aucun contrôle sur les variables environnantes et la biomasse des organismes n'est exercé, ce qui nous permet d'obtenir un portrait réel de la dynamique des communautés, à un environnement plus contrôlé au volet 3, qui nous permet de bien cerner les variables et les mécanismes à l'étude, mais au prix d'un réalisme réduit. Toutefois puisque les assemblages réalisés sont représentatifs des communautés naturelles, il est possible de s'en servir comme modèle et d'en reporter les résultats sur des communautés naturelles. En effet, les mécanismes mesurés en mésocosmes sont présent en milieu naturel, ils sont juste masqués par les facteurs abiotiques tels que la température et la dessiccation.

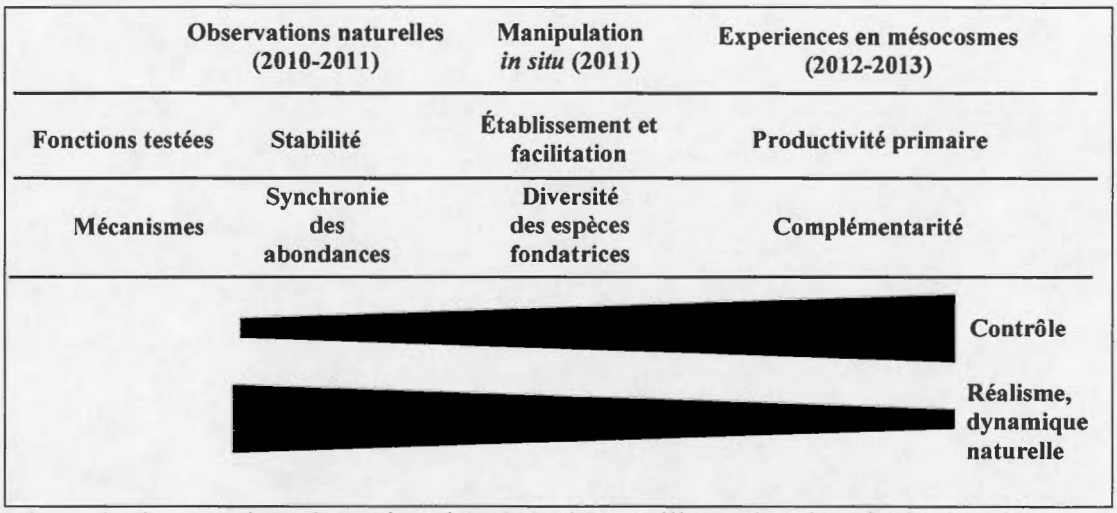


Figure 1 : Comparaison des trois volets de la thèse et illustration du gain du contrôle des variables au prix d'une perte du réalisme et de la dynamique naturelle.

## IMPORTANCES DE LA RECHERCHE

Le milieu benthique intertidal possède une grande diversité et joue un rôle important dans le cycle de la matière, des nutriments et sert de milieu tampon entre les environnements aquatiques et les environnements terrestres (Covich et al. 2004). Selon plusieurs scénarios prévisionnels du GIEC (Underwood 1989, ACIA 2004), d'importants bouleversements au niveau de l'océanographie physique et chimique sont attendus. Une augmentation des températures de l'eau et du niveau des mers ainsi que la disparition des glaces de mer protégeant les côtes contre l'effet des

vagues vont entraîner des changements dans les communautés benthiques pouvant modifier leur dynamique. On s'attend à ce que ces changements provoquent des modifications dans la structure des abondances et l'identité des espèces avant qu'une perte de la diversité ne se fasse sentir (Hillebrand et al. 2008). D'autres recherches sont nécessaires pour mieux comprendre comment une modification de la diversité peut affecter le fonctionnement des écosystèmes, et plus spécifiquement, en ce qui a trait au fonctionnement des communautés.

Ce projet de thèse innove en abordant individuellement le rôle des facteurs d'abondance, de l'identité, de la richesse et surtout de l'équitabilité des espèces sur la stabilité temporelle, la structure et les mécanismes des communautés de la zone benthique intertidale. Cette thèse génère des résultats importants en écologie fonctionnelle et ajoute un éclairage sur les liens entre la biodiversité et le fonctionnement des écosystèmes. De plus, elle contribue à la compréhension des facteurs biotiques responsables de la variabilité naturelle des populations qui est vitale pour prédire les tendances dans les propriétés des assemblages et ainsi préserver l'intégrité des produits et services rendus par les écosystèmes marins côtiers.

Dans la prochaine section, quelques notions de base sont présentées pour bien comprendre les fonctions et processus qui font l'objet d'une attention particulière dans cette thèse.

## INTRODUCTION AU CONCEPT DE LA BIODIVERSITÉ

Le terme **biodiversité**[1] vient de la contraction des mots « diversité biologique » qui a probablement été mentionné pour la première fois par Walter G. Rosen lors de la planification en 1986 du forum « national forum on biodiversity » qui a eu lieu

[1] Tous les termes en gras dans le texte sont définis dans le tableau 1, à la fin de l'introduction.

quelques années plus tard en 1995 (Magurran 2012). La biodiversité est définie comme étant la variabilité des organismes à l'intérieur d'un habitat définie. Ceci comprend la variabilité inter et intra-spécifique. Cependant, la **diversité** est souvent décrite de façon plus simpliste en terme de richesse soit le nombre d'espèces dans un habitat délimité ou à l'intérieur d'un assemblage. Cette définition de la diversité sert surtout à des fins de recensement afin d'identifier les endroits que l'on appelle « hotspot » où la diversité est plus élevée. Toutefois, à l'intérieur d'une communauté, chaque espèce ne possède pas la même abondance. Bien souvent, quelques espèces vont dominer et la majorité des autres espèces sont plus rares. La définition en terme uniquement de richesse est donc incomplète, car il manque un paramètre de répartition des abondances.

Il est maintenant établi dans la littérature que la diversité comporte deux composantes majeures soit la **richesse** et l'**équitabilité** (Nijs and Roy 2000, Wilsey et al. 2005, Magurran and McGill 2011). La richesse, comme mentionnée plus haut, est le nombre d'espèces présentes à l'intérieur d'une communauté. L'équitabilité est une mesure de la répartition des abondances des espèces dans une communauté (Smith and Wilson 1996). Le concept de répartition d'abondance est introduit dans la littérature depuis un certain temps (Preston 1948) et souvent en étudiant son opposé, la dominance (Whittaker 1965, Dayton 1975). Le terme équitabilité lui-même est plus récent et a été introduit graduellement dans la littérature grâce à des travaux de recherches tels que ceux de Weiher et Keddy (1999) Poley et coll. (2003), Smith (1996) et plus récemment par exemple, ceux de Maggi et coll. (2009). Une communauté est dite équitable lorsque les populations ont la même abondance. À l'inverse, il y a dominance lorsqu'une ou quelques espèces ayant une forte abondance dominent sur les autres plus rares.

La richesse et l'équitabilité ont des implications différentes dans le fonctionnement des communautés (Stirling and Brian Wilsey 2001, Wilsey et al. 2005) et devraient être traitées séparément (Whittaker 1965, Weiher and Keddy 1999, Nijs and Roy

2000). Par exemple, l'effet de richesse (augmentation de la richesse) augmente le nombre de traits fonctionnels dans la communauté (Tilman 1996). De son côté, l'équitabilité va influencer l'effet de la richesse en contrôlant la représentation de chacun de ces traits dans la communauté (Doak et al. 1998, Polley et al. 2003).

De façon générale, la diversité permet d'augmenter l'efficacité de certaines fonctions (c.-à-d. processus reliés à la performance) de l'écosystème et d'en assurer le maintien en cas de perturbation via plusieurs mécanismes qui seront décrits subséquemment. Bien que certaines espèces peuvent être considérées comme redondantes, chaque espèce possède tout de même des traits fonctionnels qui lui sont spécifiques lui permettant de répondre à une perturbation et d'exploiter son habitat de façon unique. Ce faisant, plus il y a d'espèces meilleur sera le fonctionnement de l'écosystème. Ce principe implique que l'identité des espèces a un rôle majeur dans le fonctionnement d'un écosystème (O'Connor and Crowne 2005, Danovaro 2012).

L'importance de la diversité peut également être démontrée en utilisant une théorie décrite dans la littérature comme l'**hypothèse d'assurance** *(*« insurance hypothesis » sensu Yachi et Loreau 1999). À l'origine, il a été démontré qu'une plus grande diversité fournit plus de réponses adaptatives aux fluctuations de l'environnement et donc une stabilité accrue des communautés (MacArthur 1955). L'hypothèse d'assurance repose sur cette redondance des espèces. Les espèces dites redondantes possèdent des traits fonctionnels similaires et ont la même fonction écologique (Walker 1992, Griffin et al. 2009b). Plus la diversité est élevée, plus les chances d'avoir des espèces avec des fonctions redondantes sont élevées. Cette redondance revêt une grande importance, car elle tamponne les effets négatifs que pourrait entrainer une perturbation naturelle ou une perte d'espèces. En effet, les espèces redondantes peuvent se remplacer ou compenser pour une espèce délogée ou disparue lors d'une perturbation sans conséquence sur le fonctionnement de l'écosystème ni sur la stabilité (Walker 1995, Griffin et al. 2009b). Les travaux de Yachi et Loreau (1999) portent sur l'effet d'assurance. Ils démontrent que l'effet tampon engendré par redondance des espèces réduit la variabilité temporelle de la production et augmente

la productivité moyenne de la communauté (complémentarité/overyielding). Une des fonctions des macroalgues marines, par exemple, est d'offrir une protection à plusieurs organismes contre la prédation ce qui permet le maintien d'un certain niveau de diversité dans le milieu. Toutefois, ce ne sont pas toutes les macroalgues du médiolittoral qui possèdent la même tolérance à la dessiccation. Par exemple, si une vague de chaleur survient imposant un stress aux macroalgues. Dans le cas où plusieurs espèces de macroalgues sont présentes dans le milieu, une espèce plus tolérante peut prendre le dessus et continuer d'offrir une protection malgré le déclin des autres en abondance. Ce faisant, les espèces associées continuent de bénéficier d'une protection et le niveau de diversité est maintenu. L'effet d'assurance permet à l'écosystème de maintenir ses biens et services sur une longue période tant et aussi longtemps qu'il y aura des espèces qui pourront remplacer celles perdues (Naeem 1998).

De leur côté, Naeem et coll. (2002) ont élaboré trois modèles basés sur les travaux de Vitousek et Hooper (1994). Le but de ces modèles est de visualiser dans un graphique la trajectoire potentielle des fonctions écologiques suite à une perte de biodiversité (voir Figure 1). Le premier modèle (associé à l'hypothèse d'assurance) stipule que les espèces sont redondantes c'est-à-dire que les fonctions vont être maintenues jusqu'au point de rupture où une diminution brusque de la fonction survient, car il n'y aura plus assez d'espèces présentes pour maintenir celle-ci. Le second modèle stipule que les espèces sont principalement uniques, l'opposé du modèle d'espèces redondantes. Ici, chaque espèce a des traits qui lui sont propres qui lui permet de répondre de façon unique à un changement dans son environnement. Comme chaque espèce est unique, perdre une espèce équivaut à perdre une fonction. Dans le troisième modèle, l'impact d'une perte de la biodiversité sur le fonctionnement des communautés dépend du contexte (habitat, identité et nombre d'espèces présentes, etc.) : C'est le modèle appelé idiosyncrasique. La réponse d'une perte d'espèces n'a pas de trajectoire claire et dépend de l'identité des espèces. Par exemple, si une espèce clé est perdue, il y aura un fort déclin dans les fonctions de l'écosystème. À l'opposé, si une espèce redondante est perdue, les fonctions resteront les mêmes.

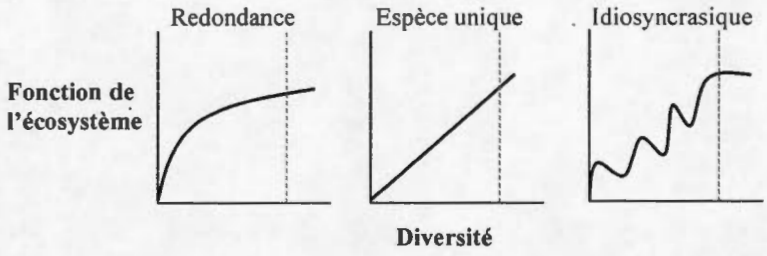


**Figure 2 :** Graphique démontrant les différentes théories des effets d'une perte de diversité sur le fonctionnement des écosystèmes. La barre pointillée représente le niveau de diversité naturelle.

## FONCTIONNEMENT DE L'ÉCOSYSTÈME

La définition de fonction de l'écosystème englobe tous les processus reliés à la performance d'un écosystème (Naeem et al. 2002, Bremner 2008) tel que le recyclage des nutriments, la production et le stockage de carbone, la résistance et la résilience des communautés et leur stabilité. Comme il est impossible d'étudier un écosystème dans son entier, il l'est étudié à plus petite échelle comme celle des communautés. Le fonctionnement des communautés possède deux aspects soit : l'aspect structurel (distribution des abondances, stabilité, identité des espèces) et l'aspect fonctionnel (les processus physico-chimiques). De plus, le fonctionnement des communautés peut être étudié à deux niveaux. Le premier niveau est biogéochimique, soit par exemple le cycle des nutriments dans un écosystème i.e. renouvellement ou la décomposition des nutriments sous la forme de matière organique (Marcus and Boero 1998). Le second niveau est biotique, soit les propriétés (pool de matière organique...), les biens (nourriture, bois...) et les services rendus à l'Homme (régulation du climat, médicaments, purification de l'eau et de l'air...). Le fonctionnement des communautés peut également être étudié en fonction de la dynamique des populations en étudiant la compétition et la prédation entre espèces ainsi que la résistance/résilience des communautés en réponse à une perturbation (Naeem et al. 2002, Bremner 2008, Magurran 2012).

Lorsque l'on parle de fonctions de l'écosystème, le terme diversité fonctionnelle est souvent employé. La diversité fonctionnelle est le nombre de fonctions que les différentes espèces peuvent fournir telles que producteur primaire, brouteurs, décomposeurs, carnivores, etc. (Hector et al. 1999). Il est alors question de group fonctionnel d'espèces soit espèces ayant la même fonction dans une communauté (Petchey and Gaston 2002). Certains travaux de recherche ont démontré qu'en intégrant les phénotypes et les traits fonctionnels des espèces ainsi que leur niveau d'équitabilité (rare ou dominante) (Wittebolle et al. 2009), il est possible d'avoir une meilleure mesure de la relation entre la diversité et les fonctions de l'écosystème et même d'identifier de nouvelles zones « hot spot », (Stuart-Smith et al. 2013).

Comme les fonctions des communautés sont très vastes et que chaque aspect peut être décrit plus profondément, je vais uniquement décrire les trois fonctions que j'ai abordées dans cette thèse soit la stabilité des abondances des assemblages au volet 1, la facilitation au volet 2 et la productivité au volet 3. Bien que la production fasse partie du volet 2 également, elle fait le sujet d'une étude plus approfondie dans le volet 3. Il ne faut pas perdre de vue le but premier de cette thèse est de mieux cerner le rôle de la diversité en termes de richesse, équitabilité, identité et abondance sur la stabilité, la facilitation et la productivité des communautés benthiques intertidales.

## STABILITÉ

Une des fonctions de l'écosystème les plus étudiées dans la littérature est la stabilité des communautés ou des populations. La **stabilité** peut être décrite en terme de **résistance** (communauté reste inchangée après une perturbation), **résilience** (temps que prend une communauté pour revenir à l'état d'origine après une perturbation) et **stabilité temporelle** des abondances ou de la productivité (l'absence de variabilité en abondance ou en productivité dans le temps) en l'absence de perturbation. Elle se mesure de plusieurs façons, mais dans cette thèse elle référera à la stabilité temporelle dans l'abondance des communautés soit :

Stabilité (St) = abondance totale moyenne / écart type

La stabilité temporelle des abondances peut être engendrée par des mécanismes biologiques, mais aussi tout simplement par un artéfact statistique. Par exemple, l'effet porte-folio (ou « statistical averaging » Doak et al. 1998, Cottingham et al. 2001, Bulleri et al. 2012) est l'un des mécanismes statistiques. L'effet porte-folio est basé sur la variation morphologique des espèces (c.-à-d. chaque espèce à des caractéristiques qui lui sont propres) qui permet de répondre de façon unique à une perturbation environnementale. Par exemple, lorsqu'une perturbation survient, une espèce peut être moins bien adaptée ou « équipée » pour y faire face et elle va diminuer en abondance. Cette diminution peut favoriser une seconde espèce plus tolérante. Ces deux espèces vont entrer en covariance négative (Schwartz et al. 2000, Griffin et al. 2009b, Valdivia and Molis 2009). Ainsi, dans un écosystème où l'asynchronie (forte covariance négative entre les espèces) est élevée, l'abondance des populations peuvent être très variables tout en ayant une abondance totale stable de la communauté. Plus il y a d'espèces avec une covariance élevée des abondances entre elles, plus l'abondance total de la communauté sera stable, c'est l'effet porte-folio. Prenons exemple sur la bourse dans le domaine financier où la notion de porte-folio est plus simple à illustrer sur la fluctuation des valeurs. La répartition des avoirs dans plusieurs actions de différents type (en opposition à l'identité d'une espèce) ce qui diminue les chances de tout perdre, car le risque est réparti dans plusieurs placements et le montant total reste plus stable. Dans le cas d'une communauté, comme chaque espèce répond de façon différente a une perturbation, si l'on augmente la richesse (le nombre d'espèces), on multiplie la variété des réponses et donc la capacité de compensation ce qui augmente la stabilité de la communauté (Ives et al. 1999, Isbell et al. 2009). L'effet de compensation est amplifié par la richesse ce qui va accroître la stabilité de la communauté.

Plus généralement, la diversité est composé de deux paramètres principaux soit la richesse et l'équitabilité. Le rôle de la richesse sur la stabilité vient d'être brièvement

décrit, mais qu'en est-il de l'équitabilité? Si une communauté est riche avec une équitabilité élevée (c.-à-d. beaucoup d'espèces présentes en abondance égale), la possibilité de réponse de la communauté face à une perturbation est accrue. En effet, lorsque l'équitabilité est élevée, il y a plus d'individus de chaque espèce, ce faisant, les traits fonctionnels de chaque espèce sont mieux représentés dans la communauté. Tout comme avec l'effet de richesse, la capacité de réponse de la communauté est accrue ce qui permet un meilleur fonctionnement. Une forte équitabilité va donc promouvoir l'effet de richesse et diminuer la variabilité dans les fonctions ou les abondances de l'ensemble de la communauté en augmentant l'effet porte-folio. Dans le cas contraire, à faible équitabilité (dans une communauté où une seule espèce domine), l'effet porte-folio est pratiquement absent, car peu d'individus de chaque espèce peuvent aider au maintien des fonctions ou compenser pour la diminution d'autres espèces (Cottingham et al. 2001).

L'effet d'équitabilité est difficile à observer dans les communautés écologiques et parfois les études n'ont pas trouvé d'effet. Par exemple, Isbell et coll. (2009) ont mis en culture des assemblages de plantes que l'on retrouve dans des prairies avec différents niveaux de richesse et d'équitabilité afin d'identifier les mécanismes contrôlant la stabilité et la productivité. Ils ont démontré qu'une plus grande richesse augmente la stabilité en augmentant l'effet d'overyielding, l'asynchronie entre les espèces et l'effet de « statistical averaging » (décrit plus loin). Toutefois l'équitabilité n'a pas eu d'influence sur la stabilité temporelle de la productivité.

## FACILITATION

La facilitation est le processus par lequel une espèce déjà établie dans le milieu permet l'établissement d'autres espèces. Bien souvent, la facilitation se fait grâce à la présence d'une espèce dite « espèce fondatrice » ou « espèces clés » qui, en modifiant les caractéristiques physiques du milieu, permet la colonisation de ce nouvel habitat par d'autres organismes. Ainsi, la facilitation découle d'interactions positives entre les organismes qui vont bénéficier de la présence d'autrui sans leur porter préjudice

(Bruno and Bertness 2001). Par exemple, le castor modifie son habitat en construisant des barrages, il crée un nouvel habitat qui peut être colonisé, entre autres, par des amphibiens. Les macroalgues telles que les laminaires vont créer des forêts marines qui vont faciliter l'établissement d'autres espèces en offrant une protection aux poissons contre leurs prédateurs ou encore, servir de pouponnières et de frayères. De même ici, la diversité va jouer un rôle. Les chances d'avoir des interactions plus fortes entre les espèces augmentent avec la diversité (Bertness and Callaway 1994, Callaway 1995, Benedetti-Cecchi 2009). Le retrait d'une espèce fondatrice peut donc avoir des conséquences directes sur la communauté en retirant, par exemple, un abri ou une protection. L'effet peut également être indirect en provoquant un effet de cascade trophique qui mènerait à une série d'extinctions d'espèces secondaires (Dayton 1975, Grabowski and Kimbro 2005, Lilley and Schiel 2006).

Il a été démontré que l'effet de facilitation est souvent couplé à l'effet d'identité des espèces (Bruno et al. 2003). Dans cette thèse, les macroalgues, *Fucus* spp. et les moules, *Mytilus* spp. sont les espèces fondatrices à l'étude. Ces organismes possèdent des traits morphologiques très différents qui vont faciliter la présence d'espèces associées qui leur sont spécifiques. Par exemple, Golléty et coll. (2008) ont mesuré chaque mois, sur une année, la production primaire et la respiration de communautés benthiques avec et sans canopée. En plus d'être les principaux producteurs primaires des zones marines, (Roman et al. 1990, Duarte et al. 2005) les macroalgues ont un rôle important dans l'établissement des organismes et sur le maintien de l'intégrité des communautés (Bertness et al. 1999).

De par leur structure, les macroalgues en milieu médiolittoral modifient leur environnement et améliorent les conditions du milieu en procurant un refuge contre la dessiccation, la chaleur et offre une protection contre la variabilité environnementale (Bertness et al. 1999). En résumé, les macroalgues améliorent les facteurs biotiques et abiotiques ce qui facilite l'établissement des organismes dans des zones qui seraient non propices à la colonisation (Bertness et al. 1999). Ces modifications de l'habitat

augmentent les chances de survie d'organismes tels que des gastéropodes et amphipodes. Quant aux moules, elles sont considérées comme des espèces fondatrices, car elles augmentent l'hétérogénéité du substrat, diminuent la force des algues et retiennent le sable (Commito et al. 2006). Ces modifications permettent l'établissement de nombreux polychètes et plusieurs autres espèces enfouisseurs (Commito and Rusignuolo 2000, Enderlein and Wahl 2004, Largaespada et al. 2012).

## PRODUCTIVITÉ

La productivité des communautés a été largement étudiée en milieu terrestre en contrastant la biomasse des espèces mise en monoculture et en polyculture. Par exemple, Tilman et coll. (2001) ont étudié l'effet de la diversité des plantes et la complémentarité dans les niches écologiques sur une période de 7 ans. Ils ont démontré que leurs parcelles expérimentales avec 16 espèces ont atteint une biomasse 2,5 fois plus grande que les monocultures. Cardinale et coll. (2007) ont également utilisé la biomasse comme mesure de la productivité en regardant les résultats de 44 expériences étudiant la relation entre la richesse et la productivité. Ils ont démontré qu'en moyenne les polycultures sont 1,7 fois plus productives que les monocultures dans 79% des expériences. Toutefois, 12% des polycultures ont une productivité plus grande que leur espèce la plus productive en monoculture (« transgressive overyielding»).

En milieu marin, la productivité a été étudiée de bien des façons. Par exemple, Griffin et coll (2009a) ont travaillé sur les macroalgues. Ils ont placé les macroalgues par groupe fonctionnel (mesure de la diversité fonctionnelle), placé les assemblages en mésocosmes *in situ*, puis ils ont mesuré la quantité d'oxygène dissout dans l'eau pour mesurer la productivité. Ils ont trouvé que l'identité des espèces présentes dans les assemblages est plus importante pour déterminer la productivité. Toutefois la diversité fonctionnelle est un meilleur prédicateur de l'effet d'overyielding que l'identité.

Les macroalgues ont un rôle important à jouer dans le cycle du carbone (Duarte et al. 2005) et pourtant l'effet d'une perte d'espèce a été peu documenté. Bruno et coll. (2005) ont étudié l'effet d'identité et de richesse sur la production primaire (taux de photosynthèse net) et l'accumulation de biomasse. Ils ont trouvé que les espèces sont toujours plus productives en polyculture qu'en monoculture indiquant un effet de complémentarité entre les espèces.

De façon générale, la diversité a un effet positif sur la productivité des communautés (Stachowicz et al. 2007). Dans les exemples d'études qui ont été démontrées plus haut, plusieurs mécanismes sont responsables de la relation entre la diversité et la productivité. Ici, je vais décrire les 3 que j'ai considéré durant mes travaux de recherche : l'effet d'échantillonnage (référé dans le texte par les termes « **sampling effect** »), la **complémentarité** et l'effet de surproduction (référé dans le texte par le terme « **overyielding** »)

## LE « SAMPLING EFFECT » ET L'EFFET DE SÉLECTION

Le « sampling effect » (SE) est visible quand une espèce possède des traits physiques qui lui donnent un avantage compétitif sur les autres espèces et sera en position de dominer la communauté. Le SE contrôle donc la relation entre la richesse et le fonctionnement de l'écosystème. Comme SE assume que seules les espèces très performantes peuvent dominer, elle est restreinte à un effet positif sur les fonctions de l'écosystème (Tilman 1999, Loreau 2000, Bruno et al. 2005). Toutefois, SE est parfois perçu comme un artefact dans les résultats de travaux de recherche masquant la relation entre la biodiversité et le fonctionnement des écosystèmes (Huston 1997). Plusieurs travaux de recherche ont tenté de trouver des façons de contourner ce problème en mathématisant SE. Cette approche est décrite dans la section décrivant l'overyielding.

Contrairement au SE, l'**effet de sélection** peut avoir un effet autant positif que négatif. L'effet de sélection a un effet négatif lorsqu'une espèce avec une production

moins élevée que les autres espèces est tout de même dominante dans un assemblage, car elle possède un taux de croissance plus élevé ou elle est plus tolérante aux conditions présentes dans le milieu (Bruno et al. 2005). L'effet de sélection et SE, ne dépendent pas de l'équitabilité des espèces (Hillebrand et coll. 2008). Qu'importe la répartition des abondances dans une communauté, ou si une espèce est plus ou moins rare, si elle possède des traits physiques qui l'avantagent, elle va dominer sur les autres. Par contre, ces deux mécanismes dépendent de la richesse. En effet, plus il y a d'espèces, plus les chances d'avoir une super espèce dans la communauté sont élevées et donc plus de chance d'avoir un effet de sélection. Par la suite, la sélection des traits de cette espèce va définir les conditions de la communauté.

## L'EFFET DE COMPLÉMENTARITÉ

C'est Woodhead (1906) qui a introduit le concept de **complémentarité** qui est basé sur la différence dans les traits fonctionnels des espèces qui entraine une séparation des niches écologiques. Chaque espèce possède des traits qui lui sont intrinsèques lui permettant d'utiliser une niche qui lui est propre (Loreau and Hector 2001, Hector et al. 2009). La proportion des niches occupées dans une communauté est le reflet des ressources utilisées dans cet écosystème. Une niche non exploitée équivaut à des ressources non exploitées ce qui diminue le rendement de l'écosystème par rapport à sa capacité maximum. Une augmentation de la diversité dans un écosystème permet de combler les niches vacantes et ainsi optimiser l'exploitation des ressources ainsi une forte diversité augmente le rendement de l'écosystème dans son ensemble (Schwartz et al. 2000). C'est l'effet de complémentarité. Il est intéressant de souligner que l'effet de complémentarité est associé avec l'effet de facilitation. En effet, comme mentionné plus haut, l'effet de facilitation va augmenter la richesse d'un milieu ce qui a pour effet d'augmenter le nombre d'interactions entre les espèces et le nombre de niches utilisées augmentant la performance de l'écosystème (Gamfeldt and Bracken 2009). En résumé, en augmentant la quantité de niches écologiques comblées, on augmente l'effet de complémentarité ce qui peut entrainer un effet d« overyielding » (Isbell et al. 2009), terme qui sera défini plus bas.

Toutefois les interactions positives entre les espèces ne sont pas toujours présentes et sont parfois même négatives. En effet, Polley et coll (2003) ont mis en monoculture et en polyculture des plantes avec différents niveaux d'équitabilité et de densité afin de définir le rôle de l'équitabilité dans l'effet de sélection et de complémentarité. Ils ont trouvé qu'à forte densité, les monocultures sont plus productives que les polycultures probablement dues à des interactions négatives entre espèces et un effet de sélection négative envers l'espèce la moins productive.

## L'EFFET D'« OVERYIELDING »

Le phénomène d'« overyielding » (OY) se produit alors que la moyenne des propriétés d'une communauté augmente avec la diversité (Cottingham et al. 2001). Tout comme la majorité des mécanismes qui sont influencés positivement par la diversité, OY est aussi basée sur la différence entre les traits des espèces. Plus il y a d'espèces, plus de niches seront comblées et plus de ressources seront utilisées entrainant le phénomène OY.

Il y a deux types OY. Lorsqu'un assemblage d'espèces est plus productif en moyenne que l'espèce la plus productive de cet assemblage mise en monoculture il s'agit de « transgressive overyielding ». Lorsque la productivité moyenne de l'assemblage performe mieux qu'une des espèces de l'assemblage en monoculture, mais ne surpasse pas la plus productive, il s'agit d'un «non-transgressive overyielding » (Bracken and Stachowicz 2006, Hector et al. 2009). Par contre, il est possible que l'effet de richesse qui génère OY soit diminué, voire même annulé, si l'équitabilité est faible (forte dominance dans la communauté). Valdivia et Molis (2009) ont démontré que l'effet de dominance par les macroalgues semble atténuer l'effet OY ce qui pourrait expliquer la relation négative observée entre la richesse et la stabilité qu'ils ont trouvée. Par exemple, une espèce dominante contrôle la structure de la communauté en monopolisant les ressources du milieu.

Un autre exemple, Hector et coll (2002) ont étudié l'effet de OY en mettant des espèces de plantes herbacées en monoculture et en polyculture et en utilisant la biomasse comme indicateur de productivité. Leurs polycultures ont atteint une biomasse supérieure à la biomasse de l'espèce dominante dans leur polyculture et ont atteint une biomasse supérieure aux monocultures (non transgressive overyielding) et les deux étaient corrélés à une augmentation de la richesse.

L'idée d'étudier OY part de loin et n'a pas toujours eu la même définition. Price (1972) a développé une série d'équations mathématiques utilisées dans l'étude de l'évolution pour identifier les causes des changements dans l'évolution des espèces. Par exemple, selon ces équations, l'effet de sélection peut sélectionner les individus avec des traits fonctionnels performants et ainsi engendrer une meilleure production, ce qui est similaire à la théorie de l'évolution. Loreau et Hector (2001) ont repris une équation de Price pour définir à leur façon l'effet OY. Ils ont examiné comment le rendement d'une polyculture peut dévier de son rendement attendu. Le rendement attendu est la somme des rendements de chaque espèce en monoculture. Si le rendement en polyculture est plus élevé que le rendement attendu, il y a OY. Par la suite, Fox (2005) s'est basé sur les équations de Price (1970, 1972) et de Loreau et Hector (2001) pour écrire sa propre définition de OY soit le « Tripartite partition », équation qui a d'ailleurs été reprise par les travaux de Long et coll. (2007). Cette équation de OY partitionne les effets de la biodiversité en trois éléments qui ont chacun une implication écologique distincte sur la productivité d'une communauté soit « trait-dependent complementarity » (TDC), le « trait-independent complementarity » (TIC) et l'effet de dominance (DE). Le TDC et le TIC sont les effets qui ont pour origine la partition des niches entre les espèces décrites précédemment. TIC est identique à la définition de la complémentarité de Loreau et Hector (2001) qui quantifie les effets de la diversité et des interactions entre les espèces. Le TDC quantifie la différence de production entre le rendement d'une polyculture (communauté possédant plusieurs espèces) du rendement excepté des monocultures (chacune des espèces séparées). Finalement, le DE est le reflet des interactions négatives entre les espèces qui sont, de façon générale le résultat d'une

compétition. La sommation de DE et TDC est identique à l'effet de sélection décrit précédemment. Ce faisant, les travaux de Fox (2005) et de Long et coll (2007) peuvent identifier l'effet de chaque mécanisme (c.-à-d. l'effet de sélection, de la complémentarité, de la dominance et des interactions entre les espèces) sur OY.

Il est important de souligner que les mécanismes du « sampling effect », de la complémentarité et de l' « overyielding » peuvent se produire simultanément et possiblement avoir une interdépendance entre eux. Par exemple, l'effet de complémentarité est influencé par le « sampling effect ». En effet, lorsqu'une espèce prend le dessus sur les autres, elle les contrôle en utilisant de façon plus efficace les ressources du milieu ce qui entraine inévitablement un effet de dominance (Hector et al. 2009).

## DESCRIPTION DE LA ZONE INTERTIDALE BENTHIQUE DU SAINT-LAURENT

Pour tester l'effet de richesse, équitabilité, d'identité et d'abondance sur le fonctionnement des communautés, le milieu aquatique peut nous offrir un cadre unique. En plus de détenir une grande diversité, le milieu aquatique a une importance à l'échelle globale dans le cycle des nutriments et le stockage de $CO_2$ (Emmerson and Huxham 2002, Covich et al. 2004, Behrenfeld et al. 2006). Cette grande capacité de stockage de $CO_2$ peut aider à la lutte contre les changements climatiques. Pour cette thèse, le milieu benthique intertidal du Saint-Laurent marin a été sélectionné, car il présente de nombreuses qualités pour l'étude de l'impact de la diversité dans le fonctionnement des communautés. Il possède une dynamique rapide et une diversité non négligeable. Il est également plus facile de reproduire des expériences dans ce milieu et le milieu est facile à manipuler. La diversité peut également être étudiée de façon spécifique (nombre, identité et équitabilité d'espèces) ou par groupe fonctionnel (groupe d'espèces possédants les mêmes fonctions écologiques) (Duffy et al. 2007).

## DYNAMIQUE DE LA ZONE INTERTIDALE

Les mécanismes qui contrôlent la dynamique des communautés changent en fonction de la hauteur dans l'estran (Bertness et al. 1999). Dans le bas de la zone intertidale, les facteurs biotiques sont plus importants que dans le haut de l'intertidal (Menge and Lubchenco 1981). La frange infralittorale, au bas de l'estran, est moins affectée par la chaleur et la dessiccation, car elle est émergée moins longtemps. Ces conditions plus clémentes permettent d'avoir plus d'espèces ce qui entraîne de la compétition et plus de relations de type prédateur/proie ou brouteur/algue. Dans le haut de la zone intertidale, le contraire se produit. Alors que les organismes sont les premiers à être émergés et les derniers à immerger, les facteurs abiotiques (chaleur/dessiccation) y sont plus importants et contrôlent la présence des organismes favorisant ceux plus tolérants aux conditions extrêmes. De ce fait, la richesse y est moindre et la compétition et la prédation sont pratiquement absentes (Watt and Scrosati 2013).

Un des phénomènes responsables de la dynamique des communautés est l'abrasion par les glaces, mieux connu dans la littérature sous le nom anglais « ice scouring ». Au printemps lors de la fonte des glaces, ces dernières de retirent en raclant les organismes au sol. Cette abrasion provoque un phénomène de succession plus ou moins important d'un printemps à l'autre (Archambault and Bourget 1983) ce qui entraîne une certaine instabilité des communautés et peut masquer l'effet des facteurs biotiques (richesse, identité...) sur le fonctionnement des communautés. De façon générale, les algues vont atteindre leur stade de maturité vers la fin de juin (Archambault and Bourget 1983). L'établissement d'une communauté bien structurée de moules peut prendre quelques semaines à la fin du printemps et début de l'été. Toutefois, dans certains cas, cet établissement de moules peut prendre toute la saison de croissance (Cusson and Bourget 2005). Pour voir un effet des biotiques sur le fonctionnement des communautés, il faut attendre que les communautés soient matures ce qui peut prendre un certain temps.

Les 2 sites d'étude sont situés sur la rive sud de l'estuaire du Saint-Laurent à Sainte-Flavie N48°37'42,5" W048°11'55,7" et à Saint-Ulric N48°48'36.8" W067°38'38.6". Il y a 48 km de distance entre les deux. Ce sont des zones intertidales rocheuses, avec la même exposition modérée aux vagues, ils ont les mêmes espèces et ne sont pas influencés par des apports importants d'eau douce (Guichard and Bourget 1998). La salinité de l'eau varie entre 28-30 PSU. Le système marin de l'estuaire du Saint-Laurent est considéré comme un environnement subarctique, car la température de l'eau varie 4°C et 15°C durant l'année en surface. Les communautés benthiques de la zone intertidale à l'étude sont exposées à des épisodes d'abrasion par les glaces (Archambault and Bourget 1983). On a identifié un total de 49 espèces soit 17 algues et 32 invertébrés. Les trois espèces les plus abondantes sont les deux macroalgues *Fucus distichus edentatus* et *Fucus vesiculosus* et les moules bleues composées de *Mytilus edulis*, *M. trossulus* et leurs hybrides. Les deux espèces brouteurs les plus abondantes sont *Littorina obtusata* et *Littorina saxatilis*. Voir les tables dans les chapitres 2 et 3 pour une liste complète des espèces.

**Tableau 1 : Définition des termes en gras de l'introduction qui seront à l'étude dans cette thèse**

| | |
|---|---|
| **Hypothèse d'assurance « Insurance hypothesis »** | Les espèces à l'intérieur d'un écosystème peuvent se remplacer les unes les autres. L'hypothèse assume également que les espèces utilisent des niches différentes ce qui leur permet de répondre de façon différente aux fluctuations de leur habitat. (Griffin et al. 2009b) |
| **Facilitation** | La présence d'une espèce va modifier les conditions de l'habitat et faciliter l'établissement d'autres organismes. (Callaway 1995) |
| **Stabilité de l'écosystème** | Probabilité que toutes les espèces persistent dans le temps. (Walker 1995) |
| **Stabilité temporelle** | Pour une communauté, peut représenter l'absence de variation en abondance totale. (Tilman 1999 ; McCann 2000; Cottingham et al. 2001). |
| **Résilience** | La capacité ou la mesure de la vitesse à laquelle un écosystème va retrouver son état d'origine après une perturbation (McCann 2000; Loreau et coll. 2002; Stachowicz et al.2007) ou, pour une communauté, le taux de renouvellement des populations après une perte égale dans toutes les populations ou compartiments (Griffin et coll. 2009). |
| **Résistance** | Pour une communauté est sa capacité à maintenir son état actuel ou à résister aux changements face à une perturbation physique (Farrell 1988; Stachowicz et al. 2007) ou un envahisseur (McCann 2000). Équivalent au terme d'inertie proposé par Underwood (1989). |
| **Production** | Taux actuel d'incorporation de la matière organique ou de l'énergie (Cusson 2005). |
| **Richesse** | Nombre d'espèces (ou groupes taxonomiques) dans une communauté ou écosystème. Elle ne tient pas compte de l'abondance relative des populations. (Stachowicz et al. 2007, Magurran and McGill 2011) |
| **Diversité** | Comprends le nombre d'espèces et leur abondance relative (équitabilité). (Stachowicz et al. 2007, Magurran and McGill 2011) |
| **Biodiversité** | Regroupe tous les organismes à tous les niveaux trophiques. Incluant les gènes, les espèces, les groupes fonctionnels et écosystèmes. (Stachowicz et al. 2007, Magurran and McGill 2011) |
| **Effet de richesse** | Il y a effet de richesse lorsqu'une communauté diversifiée diffère dans les fonctions de l'écosystème par rapport à la moyenne des fonctions des valeurs des monocultures. (Stachowicz et al. 2007) |
| **Équitabilité** | Indice qui mesure le degré d'équilibre dans l'abondance entre les espèces d'une même communauté. (Magurran 2004) |
| **Effet d'identité ou de composition « Identity or composition effect »** | Décrit les variations entre les espèces ou la combinaison des espèces et leur influence sur le fonctionnement de l'éco. (Stachowicz et al. 2007) |
| **Effet d'échantillonnage « Sampling effect »** | Augmentions des chances d'inclure une espèce plus productive lorsque la diversité est élevée qui va dominer la communauté (Hector et al. 2002). L'effet de sélection est identique, mais permet à une espèce moins productive d'être dominante (Bruno et al. 2005) |
| **Surproduction « overyielding »** | Se produit lorsqu'un assemblage d'espèce performe mieux qu'une monoculture. C.-À-D. lorsque les propriétés d'une communauté sont plus élevées en polyculture qu'en monoculture. (Cottingham et al. 2001) |
| **Complémentarité** | Résultat de la différentiation des niches qui permet une meilleure utilisation des ressources et une augmentation de la productivité (Woodhead 1906, Hector et al. 2009) |
| **Porte-folio ou « Statistical averaging »** | La somme de plusieurs variables indépendantes est moins variable qu'une seule variable. Il y a une augmentation de la stabilité des abondances et/ou de la productivité de la communauté (Griffin et al. 2009b). |

# CHAPITRE 2: VOLET 1,
# LA STABILITÉ

# SEPARATE EFFECTS OF RICHNESS AND EVENNESS ON COMMUNITY STABILITY

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**Abstract**

Previous studies have demonstrated that a high diversity within a community should enhance ecosystem functions and services. These results have stimulated further research exploring the relationship between diversity and the stability of various community characteristics. Here, we explore the links between the stability (temporal variation) of abundance and both species richness and species evenness within intertidal benthic communities. Over the course of two years and at two distinct sites, we surveyed 40 plots having a range of evenness values for the macroalgae. Our results showed that the relationship between stability and species richness will vary depending on the time (season vs. year) and space (separated vs. grouped sites) scales studied. Evenness had a negative effect on stability only at a regional scale (two grouped sites). The role of asynchrony among species, especially among macroalgae, was identified as a key mechanism affecting stability in these communities. This study helps to understand the separate roles of diversity components on temporal stability within a given community and highlights need of long time–series analyses to ensure special care is taken when considering the influence of various scales of space and time.

**Key word**: stability, biodiversity, ecosystem functioning, richness, evenness

## Introduction

The link between diversity and temporal stability (here defined as the inverse of the variation in community total abundance) is one of the main topics in biodiversity and ecosystem functioning and has been studied for a long time starting with May (1972), MacArthur (1955) and McNaughton (1977). These initial studies applied mathematical models to explain how a more complex system is indeed more stable than a simpler system. Those models provided the groundwork for further research on the relationship between diversity and ecosystem functioning. Later, Tilman et al. (1999) among many others, showed that the compensatory dynamics induced by competitive compensation and complementarity were the basic mechanisms behind this diversity-stability relationship. However, there remain some contradictory and diverging results that have raised concerns about how a change in biodiversity might influence this diversity-stability relationship (Loreau et al. 2002, Stachowicz et al. 2007, Cusson et al. 2014). Part of the contradiction might arise from the definition of diversity *per se*. Indeed, diversity has two main components: richness (the number of species) and evenness (the distribution of abundance among species) (Hooper et al. 2005). Each component has a different impact on community stability (Wilsey et al. 2005, Stachowicz et al. 2007, Soininen et al. 2012). As changes in dominance structure are thought to occur prior to any loss in diversity, the impact of evenness should priories in biodiversity ecosystem functioning studies (Hillebrand et al. 2008).

Asynchronies among species' populations within communities induce stability due to compensation dynamics (Yachi and Loreau 1999, Valdivia and Molis 2009, Sasaki and Lauenroth 2011). Therefore, the more species that are present in the community, the better the chances that the variation among species will average out (the statistical averaging effect) promoting stability within the community (May 1973, Valone and Hoffman 2003). This is explained by each species responding in a different manner to environmental factors. As they are often in competition with each other, their differing responses result in a negative covariance among them (Tilman 2000, Valdivia and Molis 2009). The compensatory dynamics allows for other mechanisms

to occur such as statistical averaging (or the portfolio effect). Statistical averaging is seen in communities when a characteristic at the community level (e.g. total abundance) is, on average, less variable in time or space than at the species level when taken separately (Doak et al. 1998, Griffin et al. 2009).

A majority of studies looking at biodiversity and its impact on stability were conducted using species richness as the main diversity component while few have looked at community evenness (Cusson et al. 2014). The effect of evenness on community stability is more difficult to describe as it primarily influences the mechanisms that promote stability rather than stability itself. For instance, in a community having low evenness, a dominant species might control resource availability that in turn leads to a negative response for the stability-diversity relationship (Steiner et al. 2005, Valdivia and Molis 2009). On the other hand, high evenness in a community would increase the number of specific roles for the species within the community. This would increase the compensatory effects and statistical averaging, and thereby minimize the impact of a perturbation on stability (Cottingham et al. 2001, Wittebolle et al. 2009). The effect of evenness on stability following a given perturbation may also vary over time as recolonization occurs. This is shown through Grimm's (1998) mass ratio hypothesis, which stipulates that over the short term, dominant species will control the stability of the community. However, over the long term, rarer species will play a greater role in community stability. As such, even rare species may thus have a major impact on ecosystem properties through this insurance hypothesis. Knowing first that diversity components (richness and evenness) have different roles in regard to temporal stability and second that their effects may change over time and space, there is a need for research targeting the effects of both richness and evenness on community stability.

Among the criticisms of biodiversity ecosysystem functionning (BEF studies), some researchers point to results coming solely from simulation models, or the use of unrealistic communities, used of random species scenario of extinction, or using

mesocosms that may not represent real life conditions (Gamfeldt and Hillebrand 2008). To overcome this criticism more field studies are needed in order to disentangle the effects of richness and evenness on community stability (Stachowicz et al. 2008). In this paper, we aim to examine the role of species richness, evenness and asynchrony on the temporal stability of abundance within subarctic intertidal communities over the course of two growing seasons at two different sites. As the various outcomes of previous studies may be related to community analysis at different scales of time and space (Dunstan and Johnson 1998, Stachowicz et al. 2008), we assess our results at different temporal and spatial scales (Vasseur and Gaedke 2007). We use data from an intertidal benthic community characterized by fast temporal dynamics and significant small-scale interactions that are easily traceable. We hypothesize that greater richness and evenness should promote temporal stability in total abundance within the community while synchronicity among populations will lead to a decrease in stability. This study should provide new ideas on the short and long-term variability within a subarctic community and whether diversity components are important for structuring community properties.

## Methods

### Site description

The study area is located on the south shore of the Saint-Lawrence Estuary, at two sites separated by 48 km (Sainte-Flavie (SF), 48°37'42,5" N ,048°11'55,7" W and Saint-Ulric (SU), 48°48'36.8" N, 67°38'38.6" W). Both sites share similar species (and having similar species' densities), have similar wave exposure (moderately exposed) and are not strongly influenced by important freshwater tributaries (Guichard and Bourget 1998). They are representative of a subarctic flat rocky shore habitat subjected to ice-scouring during winter and early spring (Archambault and Bourget 1983, Bergeron and Bourget 1984). Temperature and salinity range from 4 to 16°C and from 24 to 29%, respectively (Fradette and Bourget 1980, Archambault and Bourget 1983). The intertidal fauna and flora are characteristic of a moderately wave-disturbed environment (Archambault and Bourget 1983). The shores of the estuary

are often covered with ice during the winter (mid-December until the end of March); the ice sheet providing protection to biological assemblages against extreme cold. The ice, however, may also act as an indiscriminate disturbance factor on the flat rock surfaces and exposed crevices through heavy ice scouring (Bergeron and Bourget 1984, Aberg 1992, McKindsey and Bourget 2001).

**Community sampling**

At each site, twenty 30 x 30 cm plots, located in the mid-intertidal zone, were marked using stainless steel screws. All plots were situated within zones having abundant fucoids (>80% total cover of macroalgae). In order to test for the effect of evenness on temporal stability, at each site 10 plots were selected to represent a "low evenness" of habitat forming species (~80% cover of *Fucus distichus edentatus*, ~20% *Fucus vesiculosus* and ~20% *Mytilus* spp.). The other 10 plots were considered as having a "high evenness" of habitat forming species (about ~60% *Fucus distichus edentatus*, ~40% *Fucus vesiculosus* and ~20% *Mytilus* spp.). Since we did not manipulate the community, the evenness changes through the experiment. The selection of these plots allows us to include all community types and have a full representation of these sites in our analysis. As the plots were left unmanipulated, proportions of habitat forming species naturally changed overtime and cannot be considered as fixed factors in the data analysis.

Non-destructive visual estimates of abundance as percentage cover of all identified (> 1 mm) taxa (usually species level) for each plot were conducted on six occasions during the growing season of 2010 (June, August and October) and 2011 (May, July and September). By doing so we get the beginning of the growing season to the pic of growth in July and the start of the deterioration of the algae to frost bite in late September. The percentage cover of macroalgae and mussels was estimated through the division of each 30 x 30 cm frame into 25 equal squares, thus each square representing 4% of the total quadrat cover. This latter procedure is common (Dethier et al. 1993, Lemieux and Cusson 2014, Joseph and Cusson 2015 in final revision) and

use of the same unit among abundance estimates is necessary in order to assess the community dominance profiles in our treatments. For each plot, all organisms present at the time of sampling were counted. For very abundant littorinids, percentage cover was evaluated in the field by placing them side to side on a surface that represented 4% of total cover and then returned into the plot. The cover of the other species was evaluated by estimating an arbitrary 0.25% for each individual. As the macrobenthic community can have multiple layers, the total percentage cover for all species is not restricted and can exceed 100%. This total percentage cover can then be used as a measure of total species abundance.

The species richness represented the total number of species while evenness was estimated by the Pielou *J* » index. The latter index varies from 0 (low evenness, high dominance) to 1 (high evenness, no dominance). The temporal stability was estimated using the variability of total abundance (sum of all species percentage cover in a plot) over 3 (1-season) or 6 (2-seasons) sampling dates. Temporal stability was calculated as the average total abundance·standard error$^{-1}$. This estimate is the inverse equivalent of the coefficient of variation (CV= deviation·mean$^{-1}$) used for exemple by Tilman (1999). The term "stability", referring to temporal stability of total abundance, will be used throughout the text and figures. Synchrony ($\varphi_x$) over time among species was estimated following the equation of Loreau et Mazancourt (2008):

$$\varphi_X = \frac{\sigma^2{}_{xT}}{(\sum_i \sigma^2{}_{xi})^2}$$

where $\sigma^2_{xi}$ and $\sigma^2_{xT}$ are the temporal variance in abundance (percentage cover) of species *i* and the community, respectively. This equation does not make any assumptions about the magnitude or distribution of the species abundance thus allowed the use of empirical data.

**Data analysis**

In order to test the potential effects of spatial scale resolution on the relationship between diversity components and stability, data were analysed i) separately by year and by site; ii) site separately for two years; iii) years separately, both sites together, and iv) both sites and both years together. The relationship between stability and richness, evenness and synchrony was determined through linear regression. Differences in species richness and evenness between years and sites were assessed using ANOVA. Graphical examination of the residuals ensured that the data conformed to ANOVA assumptions (Quinn and Keough 2002). No data transformations were necessary. The community structure and composition (square-root abundance transformed) were compared among sites using the Bray-Curtis similarity index through a permutational multivariate analysis of variance (Anderson et al. 2008). These data were visualized using nMDS. In some cases, when a low number of permutations were possible, Monte-Carlos p-values were used (Anderson 2005). The contribution of each species to the average Bray-Curtis dissimilarity among treatments was also assessed (SIMPER analyses, PRIMER). A second set of analyses were performed on the species functional group (based on the species feeding habits, see Table 2). A third set of analyses were conducted using the associated species, (i.e. the canopy species were removed from the analyses in order to assess the synchrony and stability of the associated species). Linear regression and ANOVA were performed with JMP 10.0 (SAS ® Institute, Cary, NC) while multivariate analyses were performed using PRIMER+PERMANOVA 6.1 (Plymouth Marine Laboratory, UK). A significance level of $\alpha = 0.05$ was applied to all statistical tests.

**Results**

**Community description**

Note that in SF, one plot was not found over the course of 2 sampling dates. We identified a total of 39 species (17 algae and 22 invertebrates, see list in supplementary material (Table 2) with an average species density per plot of $9 \pm 0.20$

species for Saint-Flavie (SF) and 10 ± 0.18 species for Saint-Ulric (SU) ($F_{1,236}$=30.91; $p$<.0001). Both sites, SF and SU, had similar community composition (average dissimilarity between samples of each site = 33%; Pseudo-$F_{1,20}$ = 6.9586; $p$ = 0.001). There was a small difference between the sites in terms of total abundance cover ($F_{1,236}$=8.2885; $p$=0.0044). The main species responsible for dissimilarity between sites were *Fucus vesiculosus*, *Mytilus* spp., *Ralfsia clavata*, and *Fucus distichus edentatus* with 18%, 12% 11% and 10% of the variability explained by SIMPER, respectively. In May 2011 (date 4 in Fig. 3c), both sites suffered from intense ice scouring that affected the temporal trends in community properties (Fig 3.). This event considerably lowered the total percentage cover in May 2011 and the species abundance over the following months never recovered to the 2010 levels (Fig 3A). Interestingly, contraire to 2011, in 2010, temporal trends in diversity and evenness were not influence to this disturbance from ice-scouring showing high values at the beginning of both seasons followed by a small decline (Fig 3B,D). In 2011, the contraire take place, ice scouring cause the evenness to be higher in May and decline throughout the summer. This pattern was mainly caused by an increase of the very dominant canopy species (cf. Fig 4) that increased the evenness values in May 2011 when compared with October 2010 (Fig 3B). Indeed, the recolonization and growth of the canopy during the summer, visible by an increase in total abundance, may have lowered diversity and evenness at dates 5 and 6 due to competition (Fig 3 and 4). For both sites, evenness levels were generally higher throughout the summer in 2011 than in 2010 (SF: $F_{1,116}$ = 19.72, $p$ = 0.0001; SU: $F_{1,118}$ = 4.18,$p$ = 0.0429; Fig. 3D). In the SU site, the species richness in May 2011 was negatively affected by ice scouring however richness recovered during the sampling season reached similar levels to those of October 2010 (Fig 3C). At the SF site, richness levels remained generally low.

Functional group abundance was also analyzed. In 2010, at both sites canopy abundance cover remained high throughout the summer. The subcanopy species and ephemeral algae were almost completely absent from the community (Fig. 4). In May 2011, the average canopy cover decreased sharply at both sites, passing from 100%

cover in October 2010 to 10% in May 2011. The canopy then increased significantly from May to late September 2011, however the values did not reach the same level as observed in October 2010 (SF: $F_{5,112} = 84.29$, $p = 0.0001$; SU: $F_{5,114} = 28.86$, $p = 0.0001$) (Figs. 3 and 4). At SF 2011, annual and subcanopy algal species were more abundant in July (date 5) then decreased in abundance until October (date 6; $F_{5,112} = 4.07$, $p = 0.0019$). Encrusting algae showed the inverse pattern. For both years at SU, subcanopy and annual species were absent from the community sample. The percentage cover of encrusting algae at date 4 (May 2011) was significantly different from date 1 (May 2010) and date 6 (late September 2011: $F_{5,114} = 3.14$, $p = 0.0106$) (Fig. 4).

**Role of richness and evenness on community stability**

The relationship between stability and richness was positive over a two-year period at a local scale at SU and at a regional scale (SF and SU combined) (Fig. 5). However, over a single year, the relationship between stability and richness was not significant at either the local site or the regional scale. The relationship between stability and evenness was generally not significant except for a negative relationship observed in 2010 at the regional scale (Fig. 5).

The role of diversity components on community stability may be obscured by the dominance of the canopy species. When the canopy species (*Fucus distichus edentatus*, and *Fucus vesiculosus*) were removed from the analysis, thereby leaving only the associated species, the relationship between the stability of the associated species and the diversity components of richness and evenness became more positive (Fig. 6). Over a two-year period and one year periods in 2010, the relationship with richness was positively significant at a regional scale. Moreover in 2011, a positive relationship between richness and stability of the associated species was observed at a local scale at SU. Evenness had a positive relationship with the stability of associated species at a regional scale (both site combine) over a two year period and one year (2010). In 2011, evenness has a negative effect at SF.

**Effect of synchrony on stability**

Regardless of the temporal (individual or coupled years) or spatial (individual sites or regional groups) scales, the stability of the entire community decreased with increasing synchrony among species (Fig. 7A). This negative effect of synchrony was absent (except in 2011 at a regional scale) when stability calculations excluded canopy species (Fig. 7B).

**Diversity components and community composition and structure**

The dissimilarity of the communities in terms of composition (which can be seen as the temporal beta-diversity) was not linked to either species richness or evenness at any temporal or spatial scale considered (results not shown). Furthermore, there were no effects from the diversity components on the structure of the species » assemblages.

**Discussion**

We explored the links between the temporal stability of community abundance (percentage cover, hereafter simply "stability") and the diversity components of richness and evenness in natural field conditions. We also looked at the potential implications of species asynchrony as compensation dynamic in order to help explain our results. We expected that both richness and evenness should promote stability. Our results partially support this hypothesis. There were no links between richness and stability over a one-year period at either a local or regional scale. There was, however, a positive relationship over a two-year period at both the local and regional scales. We found a negative relationship with evenness only in 2010 at a regional scale.

Our results demonstrated that synchrony among species decreases community stability at all spatial and time scales. This result indicates that stability was promoted through temporal compensation dynamics. The temporal fluctuations in species abundance were most probably due to environmental factors. Many of our results

were context-dependent at both temporal and spatial scales, highlighting the fact that much longer time-series of data on different sites would provide more consistent answers on stability-biodiversity relationships. These aspects, important for fulfilling the gap between theoretical and empirical studies, are discussed below.

**Role of richness and evenness on stability**

In the spring of 2011, severe ice scouring occurred along the south shore of the St. Lawrence Estuary negatively affecting many community parameters at our study sites. This situation gave us the opportunity to explore relationships in two contrasting contexts: 2010 with natural temporal variability/stability among mature macroalgal communities versus 2011 marked by strong changes (recolonization/resilience) within communities reacting to a severe environmental stress. Throughout the summer of 2011, the percentage cover of ephemeral algae (included in subcanopy species) decreased while canopy species' cover (fucoids) and encrusting algae cover increased. Within the intertidal zone, ephemeral algae were unable to receive the same amount of light at low tide and therefore had more difficulties to grow under a mature macroalgal cover (Miller et al. 2011). This may explain the very low abundance of ephemeral algae in 2010. Ephemeral algae almost disappeared within our plots at the beginning of the 2011 season (McCook and Chapman 1993). Therefore, we observed a decrease in evenness during the growing season and the plot became more dominant due the competitive exclusion of the less competitive species like subcanopy species. The gradual increase in species number over the summer of 2011 may be explained by the increasing presence of the habitat forming canopy which facilitated the colonization of invertebrates (gastropods, crabs, urchins, etc). The canopy increased habitat quality and reduced the impacts from abiotic stressors such as heat and desiccation (Watt and Scrosati 2013) and also modified the habitat structure (Benedetti-Cecchi 2000, Bruno and Bertness 2001, Covich et al. 2004).

When we isolated the stability for only the associated species, the link with community richness became more positive. Richness always had a positive effect at regional scales and also at one site (SU) in 2011. The fucoid percentage cover constantly increased over the summer of 2011. On the other hand, organisms underneath the fucoids varied in a mostly asynchronous manner.

Evenness has a limiting effect on community stability and this effect changes when we looked at the whole community or only at the associated species. Our results highlighted the fact that dominance structure has an idiosyncratic effect on community stability and or associated community.

Our results demonstrated that the effect of richness and evenness might change according to the scales at which they are study and in this study, the relationships between stability of abundance either with richness and evenness seemed slightly stronger (either positive or negative trends or significant results) when combining data at the regional scale. Work from Archambault et Bourget (1996) demonstrated that more variance in species richness and can be explain by the scale (1km vs 10m) and the heterogeneity of the substrates. Care should be taken when interpreting data from linear relationship that combine different sites with different richness or evenness levels.

**Synchrony among species and community stability**

We found a strong negative correlation between species synchrony and stability. This follows expectations from theoretical (Doak et al. 1998) and empirical studies (Cottingham et al. 2001) that showed that synchronicity among species exacerbated the total abundance community variability. Inversely, the mechanism by which the asynchrony has a positive impact on the stability of the community seems to be confirmed in our study. When species fluctuate in a more asynchronous manner as richness increases, there arises a stabilisation effect on community properties including function and biomass (Downing et al. 2014). When biotic interactions (e.g.

competition) dominate within the community, there tends to be more asynchrony in population fluctuations (Grman et al. 2010). On the other hand, if environmental factors are driving the community dynamics, all species should decrease and increase at the same time and in a similar fashion. Such positive covariance is common and reduces stability within communities (Houlahan et al. 2007, Valdivia et al. 2012). In our study, the 2011 ice-scouring event affected both the abundance and richness of the community. During that year, environmental forces induced synchrony into intertidal zone populations as they were all in a recovering process, especially canopy species, producing a destabilizing effect in the community. Our results, when removing the macroalgal canopy species from analysis (Fig 5b), showed that this destabilizing effect disappears, again highlighting their strong effect on these relationships.

**Concluding remarks**

In this study we demonstrated that the effects of richness and evenness on community stability differed. Among other potential mechanisms, we showed that synchrony among populations within communities, especially when canopy species are considered, contributed to decreased community stability. The intertidal community dynamics at our sites were highly controlled by environmental stressors, notably ice-scouring. As such, environmental conditions may overcome the diversity effect on community stability as seen in comparable environments by Romanuk et Kolasa (2004) using long-term data on invertebrate populations in rock pools. Over two growing seasons, it may be difficult to disentangle separate potential effects of diversity components on community stability. However, we had the opportunity over two years of sampling, to describe the diversity-stability relationships of two contrasting seasonal dynamics in 2010 and in 2011 with natural variability among mature communities and a recovery dynamics, respectively. Our study, clearly highlighted the need to carefully set the scale, both spatial (site/regional) and temporal (season/years), at which data resolution are considered. Future studies, integrating various population dynamics within longer time-series are needed.

Nevertheless, this study also stressed the need to consider the distinction between the two components of diversity (richness and evenness) in order to provide a better understanding of stability-diversity relationships and the different mechanisms behind them.

**Acknowledgements**

We like to thank M. Gagnon, S. Cimon, P. Carrier-Corbeil, L. Joseph, W. H. Landry and H. Perelman, and V. Paradis for their precious help in the field and laboratory. This study is part of the Ph.D. dissertation of J.L. at UQAC. Financial support was provided by grants from Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants) and FQRNT (Quebec Funds for Research in Nature and Technology, new researcher's start-up program) to M.C.

# GRAPHS AND TABLES

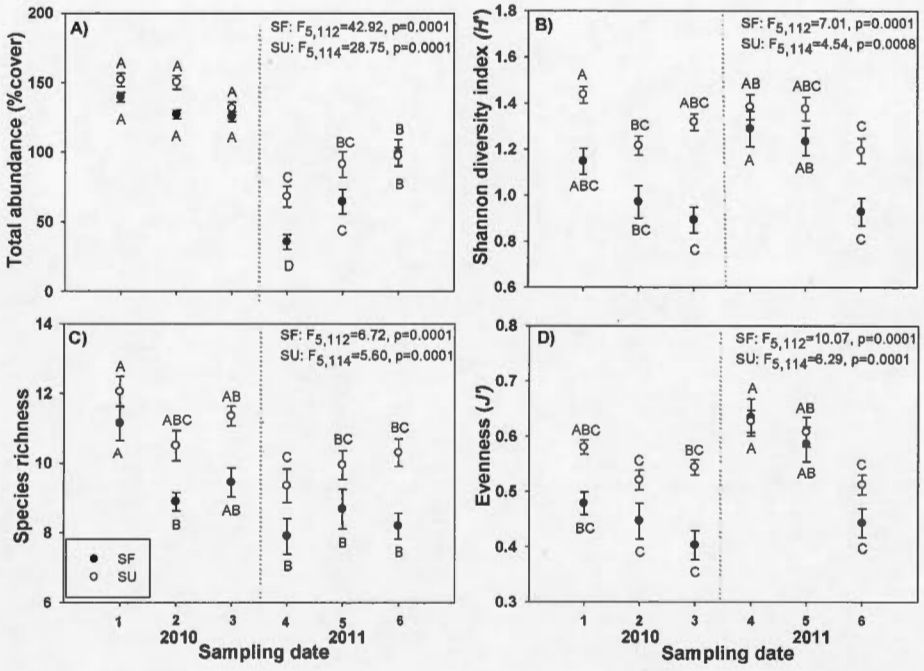


**Figure 3 :** Point bars showing average (±SE) of a) total abundance percentage cover, b) Shannon diversity index (*H'*), c) species richness and, d) Pielou evenness (*J'*) over the 6 sampling dates at Sainte-Flavie (SF, black dots) and Saint-Ulric (SU, white dots). Sampling dates occurred in June, August and October 2010 (dates 1 to 3, respectively) and in May, July and September 2011 (dates 4 to 6, respectively). Different letters above the bars represent statistically different averages among dates within sites.

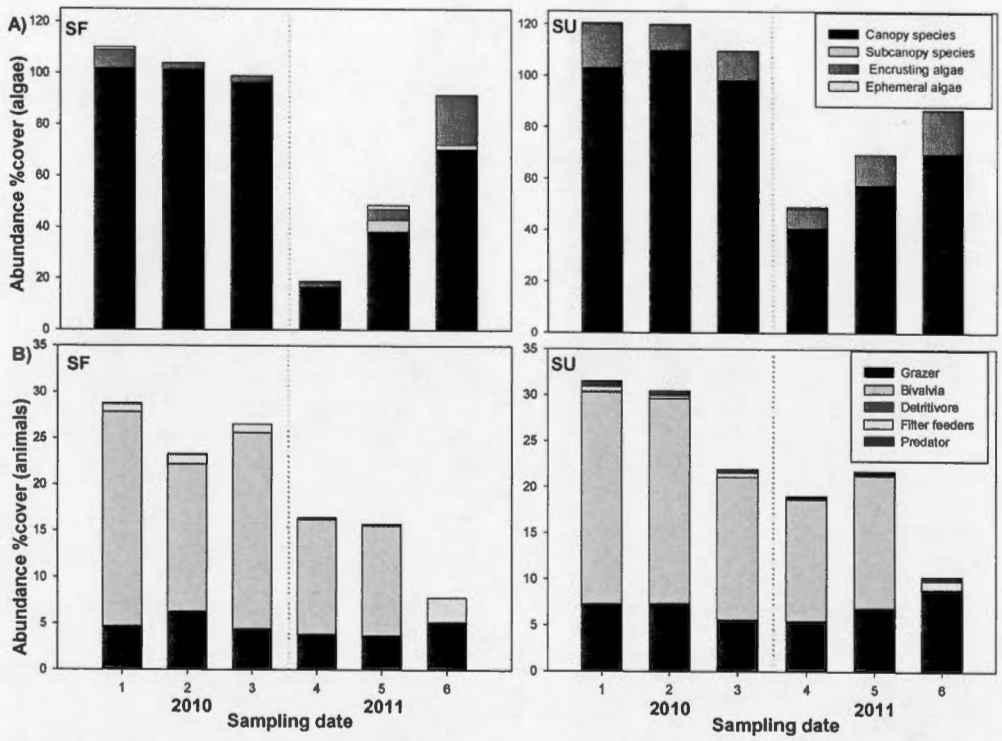


**Figure 4 :** Average total percentage cover composition over the sampling date in 2010 and 2011among functional guilds of a) algae and b) animals. Since Bivalvia includes structuring species such as mussels, they were separated from other filter feeders.

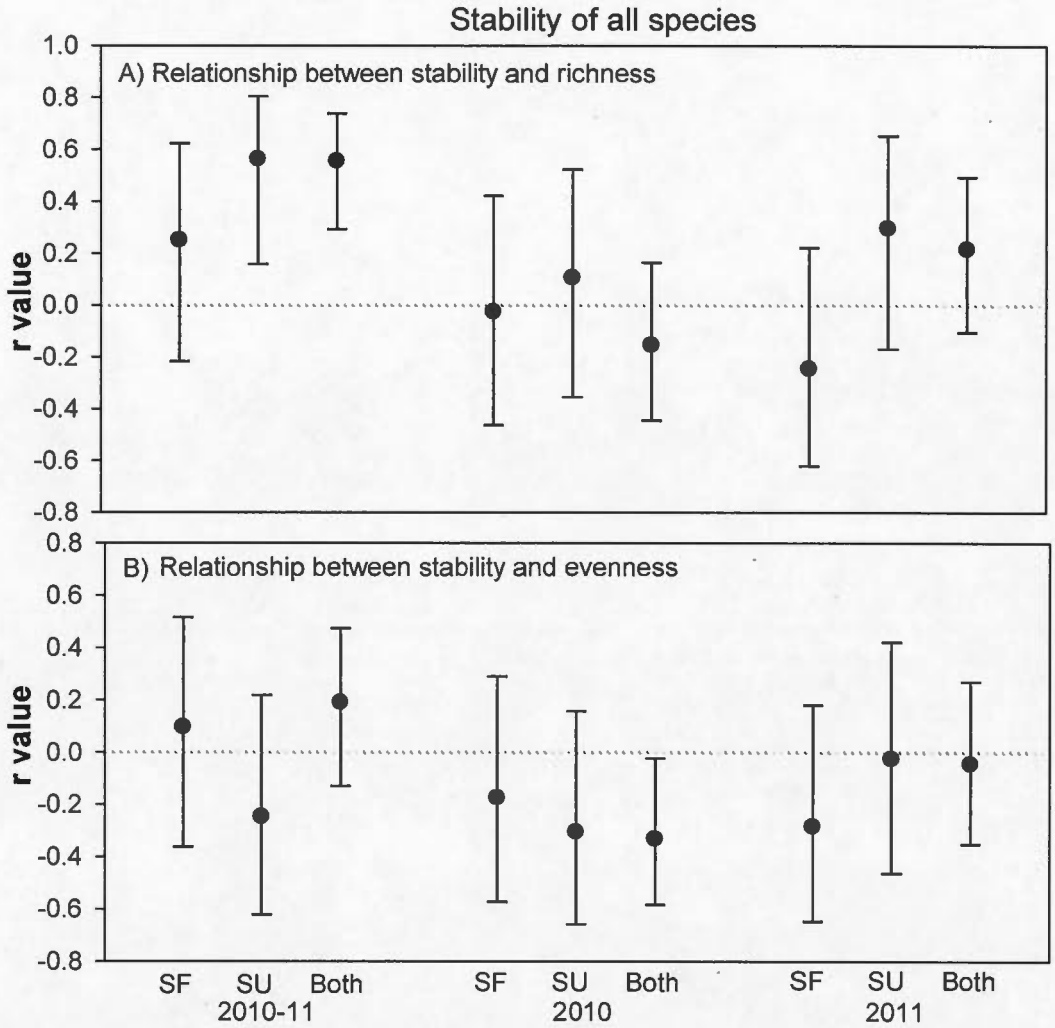


Figure 5 : Pearson correlation coefficient (average ± CI 95%) of the relationship between A) stability and richness, and B) stability and evenness (all species included). The results are shown for the individual years of 2010 and 2011 as well as combined for both years (2010-2011). Similarly, data are organized by individual site, Sainte-Flavie (SF) and Saint-Ulric (SU), as well as combined (Both) for the regional scale.

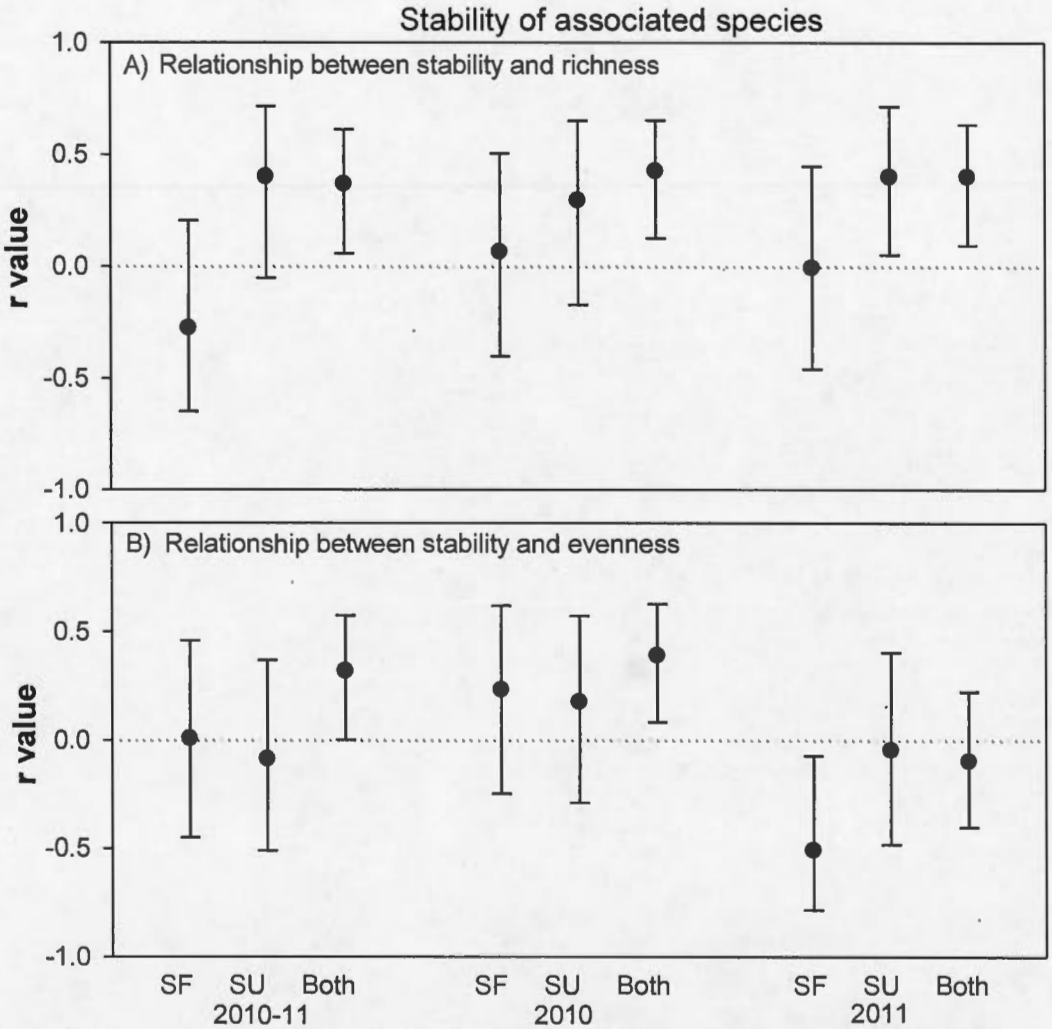


Figure 6 : Pearson correlation coefficient (average ± CI 95%) of the relationship between A) stability and richness, and B) stability and evenness. Stability, in this figure, represents only the associated species of canopy species (*Fucus* spp.) as canopy species were removed for the stability calculation. The results are shown for the individual years of 2010 and 2011 as well as combined for both years (2010-2011). Similarly, data are organized by individual site, Sainte-Flavie (SF) and Saint-Ulric (SU), as well as combined (Both) for the regional scale.

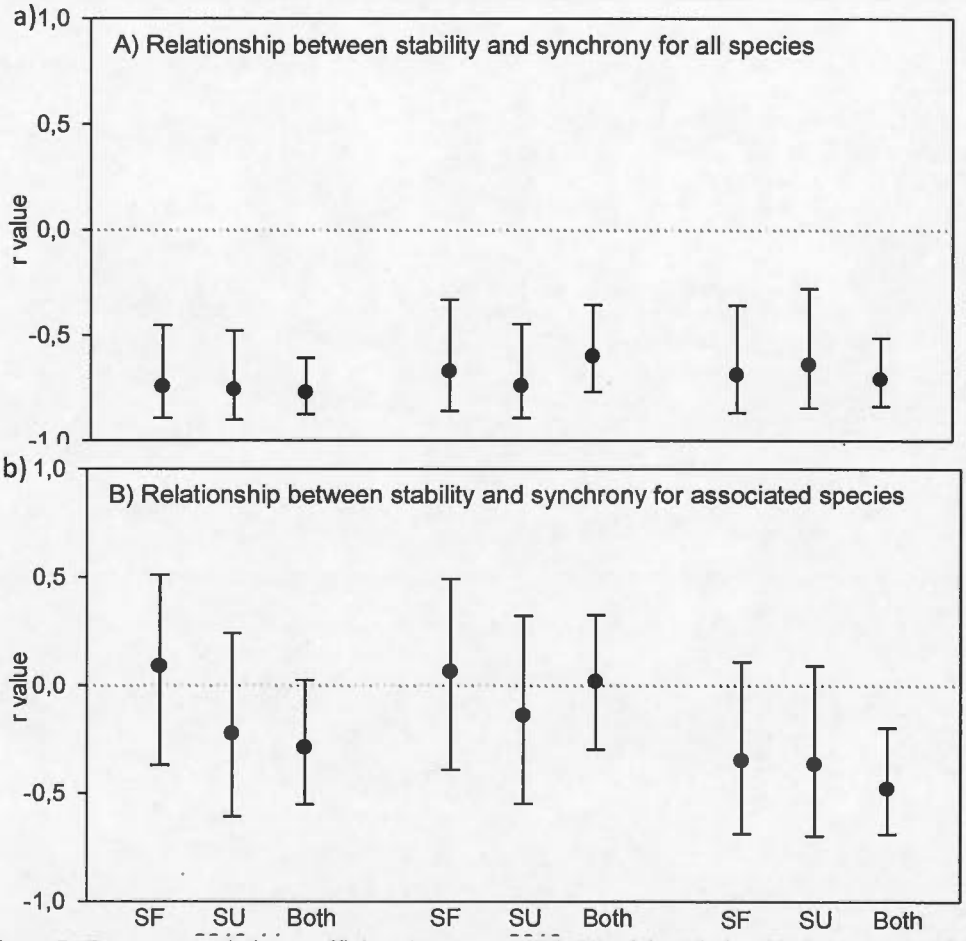


Figure 7 : Pearson correlation coefficient (average ± CI 95%) of the relationship between a) stability in total abundance and synchrony for the whole community and b) between stability in total abundance and synchrony for canopy associated species only. The results are shown for the individual years of 2010 and 2011 as well as regrouped for both years (2010-11). Similarly, data are organized by individual site, Sainte-Flavie (SF) and Saint-Ulric (SU), as well as combined (Both) for the regional scale.

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## Complementary material

Table 2 : List of species observed in this study.

| Functional group & Species | Phylum | Class | Order | Family |
|---|---|---|---|---|
| **Canopy algae** | | | | |
| *Ascophyllum nodosum* | Phaeophyta | Phaeophyceae | Fucales | Fucaceae |
| *Fucus distichus edentatus* | Phaeophyta | Phaeophyceae | Fucales | Fucaceae |
| *Fucus vesiculosus* | Phaeophyta | Phaeophyceae | Fucales | Fucaceae |
| **Ephemeral algae** | | | | |
| *Ectocarpus* spp. | Phaeophyta | Phaeophyceae | Ectocarpales | Ectocarpaceae |
| *Petalonia fascia* | Phaeophyta | Phaeophyceae | Scytosiphonales | Scytosiphonaceae |
| *Porphyra* spp. | Rhodophyta | Rhodophyceae | Bangiales | Bangiaceae |
| *Ulothrix* spp. | Chlorophyta | Chlorophyceae | Ulotrichales | Ulotrichaceae |
| Ulvaceae | Chlorophyta | Chlorophyceae | Ulotrichales | Ulvaceae |
| **Encrusting algae** | | | | |
| *Clathromorphum circumscriptum* | Rhodophyta | Rhodophyceae | Corallinales | Corallinaceae |
| *Hildenbrandia prototypus* | Rhodophyta | Rhodophyceae | Cryptonemiales | Hildenbrandiaceae |
| *Ralfsia clavata* | Phaeophyta | Phaeophyceae | Ectocarpales | Ralfsiaceae |
| *Ralfsia fungiformis* | Phaeophyta | Phaeophyceae | Ectocarpales | Ralfsiaceae |
| ***Sub canopy algae*** | | | | |
| *Spongomorpha arcta* | Chlorophytina | Ulvophyceae | Ulotrichales | Acrosiphoniaceae |
| *Chordaria flagelliformis* | Phaeophyta | Phaeophyceae | Ectocarpales | Chordariaceae |
| *Rhodomela confervoides* | Rhodophyta | Rhodophycaea | Ceramiales | Rhodomelaceae |
| *Rhodomela palmata* | Rhodophyta | Rhodophyceae | Ceramiales | Rhodomelaceae |
| *Scytosiphon lomentaria* | Phaeophyta | Phaeophyceae | Scytosiphonales | Scytosiphonaceae |
| **Filter feeders** | | | | |
| *Aulactinia stella* | Cnidaria | Anthozoa | Actiniaria | Actiniidae |
| *Balanus* spp. | Arthropoda | Maxillopode | Sessilia | Balanidae |
| *Hydrozoa* sp. | Cnidaria | Hydrozoa | | |
| *Pectinaria gouldi* | Annelida | Polychaeta | Canalipalpata | Pectinariidae |
| **Bivalvia** | | | | |
| *Mya arenaria* | Mollusca | Bivalvia | Myoida | Myidae |
| *Mytilus edulis* | Mollusca | Bivalvia | Filibranches | Mytilidae |
| **Grazers** | | | | |
| *Isopoda* spp. | Arthropoda | Malacostraca | Isopoda | |
| *Littorina obtusata* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae |
| *Littorina saxatilis* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae |
| *Littorina littorea* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae |
| *Lacuna vincta* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae |
| *Margarites helicius* | Mollusca | Gastropoda | Archaeogastropoda | Trochidae |
| *Tectura testudinalis* | Mollusca | Gastropoda | Patellogastropode | Lottidae |
| **Detrivores** | | | | |
| *Alitta virens* | Annelida | Polychaeta | Phyllodocida | Nereididae |

| | | | | |
|---|---|---|---|---|
| *Eteone longa* | Annelida | Polychaeta | aciculata | Phyllodocidae |
| Oligochaeta | Annelida | Oligochaeta | | |
| Polychaeta | Annelida | Polychaeta | | |
| *Cancer irroratus* | Arthopoda | Malacostracea | Decapoda | Cancridae |
| *Nucela lapilus* | Mollusca | Gastropoda | Neogastéropode | Muricidae |
| *Strongylocentrotus droebachiensis* | Echinodermata | Echinoidea | Echinoida | Strongylocentrotidae |

# CHAPITRE 3: VOLET 2,
# LA FACILITATION

# EFFECTS OF HABITAT-FORMING SPECIES RICHNESS, EVENNESS, IDENTITY AND ABUNDANCE ON BENTHIC INTERTIDAL COMMUNITY ESTABLISHMENT AND PRODUCTIVITY

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**Abstract**

In a context of reduced global biodiversity, the potential impacts from the loss of habitat-forming species (HFS) on ecosystem structure and functioning must be established. These species are often the main community primary producers and have a major role in the establishment of organisms through facilitation processes. This study focuses on macroalgae and mussels as HFS within an intertidal zone along the St. Lawrence estuary (Quebec, Canada). Over a 16-week period, we manipulated the *in situ* diversity profile (richness, evenness, identity, and abundance) of the dominant HFS (*Fucus distichus edentatus, F. vesiculosus*, and *Mytilus* spp.) in order to define their role in both the establishment of associated species and community primary production. Contrary to expectation, no general change in HFS richness, evenness, abundance, or identity on associated species community establishment was observed. However, over the study period, the HFS diversity profile modified the structure within the trophic guilds, which may potentially affect further community functions. Also, our results showed that the low abundance of HFS had a negative impact on the primary productivity of the community. Our results suggest that HFS diversity profiles have a limited short-term role in our study habitat and may indicate that biological forcing in these intertidal communities is less important than environmental conditions. As such, there was an opportunistic establishment of species that ensured rapid colonization regardless of the absence, or the diversity profile, of facilitators such as HFS.

**Keywords**: habitat-forming species; community establishment; evenness; diversity; primary production; marine benthos; community structure, functional response; rocky intertidal

Published in PLoS ONE:
Http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0109261

**Citation: Lemieux J, Cusson M (2014) Effects of Habitat-Forming Species Richness, Evenness, Identity, and Abundance on Benthic Intertidal Community Establishment and Productivity. PLoS ONE 9(10): e109261. doi:10.1371/journal.pone.0109261**

## Introduction

Anthropogenic activities and climate change are the main drivers of global biodiversity loss *via* habitat destruction and modification (Pimm et al. 1995, Chapin III et al. 2000, Barnosky et al. 2011). These stressors negatively affect biodiversity-ecosystem functioning (BEF) relationships by altering the interaction between species (e.g. complementarity, Tilman 1999) and decreasing habitat quality (Vitousek et al. 1997), thereby reducing ecosystem services, such as fisheries and enhanced coastal production and water purification provided by biodiversity (Hector et al. 1999). Therefore, understanding the role of biodiversity in ecosystem functioning has become one of the main areas of focus in ecology (Naeem et al. 1999, Benedetti-Cecchi et al. 2001, Balvanera et al. 2006).

Even though numerous studies have found a positive impact of diversity on ecosystem functioning (Tilman 1997, Hooper et al. 2005, Proulx et al. 2010), research results are not always consistent (e.g. Stachowicz et al. 2007). A possible cause could be related to how the identity and the dominance structure, or evenness (Grman et al. 2010), may alter how the richness affects processes and functions within a species-rich community relative to a species-poor community (Stachowicz et al. 2007). It has been argued that changes in the dominance structure (evenness) may arise prior to biodiversity loss with consequences on ecosystem functions (Hillebrand et al. 2008), including facilitation, which is a key mechanism positively influencing ecosystem efficiency through enhanced diversity (Bruno and Bertness 2001, Stachowicz 2001, Cardinale et al. 2002). Facilitation is provided by, among others, habitat-forming species (or ecosystem engineers sensu Jones et al. 1994) that create or modify habitat. Habitat-forming species (hereafter HFS) have positive impacts on species richness and abundance, play a major role in organizing community structure, and have an important function in determining community productivity (Hector et al. 1999, Jenkins et al. 1999).

In the marine intertidal zone, seaweeds (Benedetti-Cecchi et al. 2001, Crowe et al. 2013) and mussels (Commito et al. 2008) fulfill the role of HFS by increasing the complexity of these habitats (Gee and Warwick 1994). Macroalgae offer protection against physical stresses, such as waves and air exposure (Connell 1961, Scrosati et al. 2011, Valdivia et al. 2012). They also provide a suitable environment for organisms by offering shelter and protection from predation (Bruno and Bertness 2001) and desiccation (Bertness et al. 1999), as well as serving as a food source (Dayton 1975, Bruno et al. 2003). Mussel beds enhance diversity by creating a more heterogeneous substrate providing additional refuges for species to colonise (Commito and Rusignuolo 2000). Mussels also reduce wave swept impacts (hydrodynamic facilitation) allowing other species to colonize the bedrock (Enderlein and Wahl 2004).

As each HFS has a specific range of functional traits and a particular assemblage, (Begin et al. 2004, Christie et al. 2009) a community with a higher HFS abundance and richness should increase the diversity of associated species. Also, increasing evenness should enhance the representation of each HFS as well as the richness effect(Maggi et al. 2009) (Doak et al. 1998). Increasing these characteristics should influence the establishment of associated species and their diversity (Bell 1991, Haddad et al. 2001, Bates and DeWreede 2007). Therefore, habitats marked by a high abundance, richness, and evenness (equal abundance) of HFS should support a more diverse assemblage of associated species.

Primary productivity of the whole community, as an ecosystem function, could also be influenced by changes in richness (Bolam et al. 2002), evenness (Cerabolini et al. 2010), identity (O'Connor and Crowne 2005), and abundance of HFS (Roman et al. 1990). Primary production depends on the interaction of habitat complexity, shade, and nutrient enrichment (Eriksson et al. 2006), as well as algal diversity (Balvanera et al. 2006, Hillebrand et al. 2007). These characteristics will act through

complementarity (Isbell et al. 2009) and the sampling effect. The complementarity effect occurs when a greater range of functional traits in a system allows a better use of resources (Loreau and Hector 2001, Cardinale et al. 2002) by inducing better exploitation of niches and resources, thus making the whole community more efficient. Sampling effect is the natural selection of a more competitive or productive species. Increasing the richness enhances the probability of having one species that is more productive than the other species (Huston 1997).

Diversity indice is composed of both richness and evenness components (Smith and Wilson 1996, Grman et al. 2010, Magurran and McGill 2011). Disentangling their separate effects in studies of biodiversity-ecosystems functioning would be valuable. Richness and evenness have different roles in community functioning (Stirling and Brian Wilsey 2001, Wilsey et al. 2005) and should be treated separately (Whittaker 1965, Weiher and Keddy 1999, Nijs and Roy 2000). For instance, species richness is responsible for the number of functional traits (Tilman 1996), while evenness may influence the richness effect by controlling the variation of traits represented in a community (Doak et al. 1998, Polley et al. 2003). In a rich community with high evenness, the chances of having a more productive species that is well represented will be greater than in a dominant community (Mulder et al. 2004, Wittebolle et al. 2009). Moreover, evenness is known to have a positive impact on productivity by increasing the representation of each species' functional traits (Wilsey and Potvin 2000) allowing a greater complementary effect.

In this paper, we designed an *in situ* experiment to test the effects of richness, evenness, abundance, and identity of three HFS on the establishment and characteristics of the associated species and the overall community primary productivity. We used realistic changes in HFS structure in a subarctic intertidal community where pronounced climate change impacts are expected, with increasing averages and variances of water and air temperatures; changes in salinity; and a

thinner ice cover during a shorter winter period (ACIA 2004). It is anticipated that high latitude habitats will experience stronger modifications in richness, composition, and abundance of HFS (Boer et al. 2000, Walther et al. 2002, Prowse et al. 2006). We hypothesised that increasing richness, evenness, and abundance of HFS within a community will stimulate the establishment of a more diverse community of associated species by enhancing habitat complexity, facilitation processes, and productivity through better niche partitioning and complementarity. We predicted that the identity of the HFS would affect the structure of their associated assemblage and the community function (e.g. productivity) due to their own physical and biological characteristics. A better understanding of how HFS diversity profiles affect communities will allow scientists to make better predictions and give more comprehensive recommendations to policy makers.

## Methods

### Site description

The study was located in the intertidal zone near the municipality of Sainte-Flavie (48°37′42.5″ N, 68°11′55.7″ W) along a straight coast on the south shore of the St. Lawrence estuary (Province of Quebec, Canada). No field permit was required in our study location, and no threatened or endangered species were involved. The coastal substrate is composed of stable bedrock moderately exposed to waves and with limited exposure to freshwater inflow and human disturbances. The water salinity ranges from 24 to 28 PSU and the average water level is 1.17 m above the lowest spring tide level with an average amplitude of 2.5 m. The annual water temperature varies between 4°C and 15°C (St. Lawrence Global Observatory; SLGO.ca). The shore communities can be exposed to moderate or heavy ice scouring (Bergeron and Bourget 1986, McKindsey and Bourget 2001). The experimental site was located in the mid-low intertidal zone where the fucoids (*Fucus distichus edentatus* and *Fucus vesiculosus*) are the dominant species of canopy macroalgae and the benthic flora and fauna are typical of a subarctic community (Fradette and Bourget 1980).

**Experimental setup**

To test the effect of habitat-forming species evenness, richness, identity, and abundance on associated species, artificial communities were assembled *in situ* in the intertidal zone (tidal height between 0.8-0.9 m). A total of 56 polyethylene experimental grids were screwed to the bedrock with a flat surface (30 x 30 cm; square mesh of 3.2 cm), and all organisms were removed by scraping. A minimum distance of 3 m between all grids was respected and they were all located in the mid-low intertidal zone where the maximum biomass is found. Habitat-forming species (HFS) from the same intertidal level were collected to assemble artificial communities. Mature individual plants (approximate size: 15 to 25 cm) of *Fucus distichus edentatus* and *Fucus vesiculosus* were harvested nearby. These two macroalgae might be considered redundant having the same functional role. We used these specific algae due to their high abundance on the shore, and they are representative of a subarctic environment. For the blue mussels (composed of *Mytilus edulis*, *M. trossulus*, and hybrids, hereafter named *Mytilus* spp.), individuals (shell length of 2.5 to 3.5 cm) were collected from a single mussel bed about 20 km away at the same tidal height and from similar environmental conditions to our experimental site. This was done for logistical reasons as the higher abundance of similar size mussels in the adjacent site was easier to harvest and allowed us to transplant them within 12 hours. All visible epibionts on macroalgae and mussels were removed gently by hand and attached individually to the grid using plastic coated wire according to each treatment (see details below for each treatment). A total of 70 ± 5 g of mussels (about 20 individuals) was placed in 10 x 8 cm plastic mesh bags; each bag represented about 5% cover of the total 30 x 30 cm grid surface. To facilitate mussel byssal attachment and further collection of associated organisms, a rubber substrate was placed under the mussels in each bag. The bags were fixed to the grids using tie-wraps in a way to ensure that all mussel apertures were facing up.

The percentage cover of each HFS was manipulated in each grid to form different artificial assemblages resembling those observed in the surrounding communities. Six polyspecific treatments containing the three habitat-forming species were divided into two levels of total abundance; High (AH-) and Low (AL-) with ~120% and ~50% total cover respectively (sum of the % cover of all manipulated species on grid), and three levels of evenness among manipulated species; High (-JH), Medium (-JM), and Low (-JL) with obtained Pielou $J'$ index values (average ±SD) of 0.98±0.01, 0.79±0.02 and 0.56±0.03 respectively (see Table 3). A $J'$ index close to 1 means a more equal abundance among habitat-forming species, while a low value indicates dominance. Three monospecific treatments were also used with 100% cover for both *Fucus* species (FUVE, FUED) and 30% cover for the mussels (MYTI). The abundance values used in all abovementioned treatments for 3 HFS species are common for the surrounding area (e.g. individual species cover of 20-100% for both *Fucus* sp and 10-30% for mussels; Lemieux and Cusson unpublished data). *Fucus distichus edentatus* is often the dominant macroalgae at the tidal level of our experimental plots. Procedural controls with empty shells (treatment name: SHEL) in bags were used to separate the effect of the living mussels from their shells. Control plots with grids alone (without any HFS, treatment name: CONT) were also used. Finally, natural references (with at least >80% of *Fucus* spp., treatment name: NATU) were randomly sampled with a 30 x 30 cm quadrat on the same intertidal level. All treatments were randomly assigned to each grid. Six replicates were used for all polyspecific treatments and the natural reference treatments, while four replicates were used for the monospecific treatments, procedural empty shells control, and empty control grid treatments for a total of 62 experimental plots (i.e. 56 grids and 6 natural references).

The experiment began on May 14$^{th}$ 2011 and remained in place until September 4$^{th}$ 2011. Maintenance was done every two weeks to ensure that each treatment remained constant throughout the experiment. In early September, at the collecting time, visual

evaluations of the percentage cover of each observed macroscopic (>1 mm) species were recorded using a 30 x 30 cm quadrat divided into 25 squares with values of 4% cover each. The total cover can easily exceed 100% since all organisms are counted (total abundance = sum of all species % cover). Thereafter, in all experimental plots, each macroalgae, mussel bag, grid, and organism attached to the rock was collected separately, in individual bags, and brought to the laboratory. Loosely attached organisms (and associate sessile organisms on them) caught by the grids were considered separately (see results section below). In the laboratory, the HFS were gently washed with filtered saltwater over a 0.5 mm mesh sieve. All associated biota were preserved in 70% ethanol for further sorting. All organisms were identified to the lowest possible taxa level (usually species), counted, and weighed (maximum precision: 0.0005 g). Additional identified species in the laboratory were added to the field visual evaluation data. For those species, that were usually very small, we used a transformation into percentage cover by multiplying the number of individuals per species by an arbitrary value of 0.01%. All biomass values were converted into energy (kJ) using published mass-to-energy conversion coefficients (Brey 2004). No biomass was measured for the encrusting species (e.g. *Ralfsia* spp. or barnacles) due to their nature. A biomass (kJ) data set was used together with the % cover data set for further precision in community abundance structure in further univariate (e.g. evenness and diversity indices) and in multivariate analyses. Animals were classified based on their trophic guilds: Grazers: 8 species; Filter feeders: 5 species; Omnivores: 11 species (see Table 4 in supporting information section). These three groups were chosen in order to have a maximum density of species within them.

**Production measurement**

During the maximum growth period in mid-July 2011, the primary production of the whole community was measured in all treatments (three randomly chosen replicates) by monitoring the change in $CO_2$ mole fraction (ppm) *in situ* using a benthic chamber (method and devices described in Migné et al. 2002). The benthic chamber is made of

a transparent Plexiglas box, with a 30 x 30 cm base, covered with a dome; the chamber's total volume is 18 L, and it is connected through a closed circuit to a $CO_2$ infrared gas analyser (LI-COR Inc, LI-820, Lincoln, NE, USA). The data were recorded on a data logger (LI-COR LI-1400; LI-COR Inc.) every 15 seconds (mean of 5 sec data interval) during a 10 to 20 minute incubation depending on the community response. Measurements were carried out with ambient daylight (always over 1000 µmol photon/$m^2$) to measure the net primary production (NPP) and in the dark (benthic chamber covered with an opaque polyethylene sheet) to measure the respiration (R). The gross primary production (GPP) was calculated by adding NPP to R. This method was not used to evaluate the total budget of the shore community, but it gives an accurate and useful measure of primary production at the community scale in similar conditions.

**Data analyses**

All analyses were done on the community of associated species, which excluded the three manipulated habitat-forming species, except for new recruits. The data analyses were done using a two-step approach. First, a two-way ANOVA was done on the polyspecific treatments only to analyse the main fixed factors of abundance and evenness treatments and their interaction. This allowed testing for the abundance factor regardless of evenness levels and vice versa. Since none of the results were significant in the first two-way ANOVA approach, one-way ANOVA (and, consequently, one-way PERMANOVA for multivariate analyses, see below) comparing all treatments were done (fixed factor, 12 treatment levels) on total abundance (sum of species % cover or biomass in kJ), richness, Pielou evenness ($J'$), and Shannon-Wiener diversity ($H$ »; $Log_e$) for each plot. ANOVA assumptions were checked by a graphical examination of the residuals (Montgomery 1991), followed by multiple comparison tests (Tukey-HDS, unless stated) when necessary. One-way ANOVA was performed on the NPP, R, and GPP values among treatments (nine levels see results section).

The structure (using raw data) and the composition (with presence/absence) of communities and trophic guilds were compared among treatments using Bray-Curtis similarity into Permutational multivariate analysis of variance (PERMANOVA; Anderson 2005). In some cases, when only a restricted number of permutations were possible, Monte Carlo p-values (named $p_{mc}$) were used (Anderson et al. 2008). Principal coordinate ordinations (PCO) were used to visualize the multivariate data (results of the PCO in the supporting information section). The contribution of each species to the average Bray-Curtis dissimilarity among treatments was assessed (SIMPER analyses, PRIMER). Further analyses were done on the abundance among trophic guilds (e.g. Grazers, Filter feeders, and Omnivores) using the PERMANOVA pairwise test. Univariate analyses were done using JMP 10.0 (SAS ® Institute, Cary, NC), while multivariate analyses and ordinations were done in PRIMER+PERMANOVA 6.1 (Plymouth Marine Laboratory, UK). A significance level $\alpha = 0.05$ was used for all statistical tests.

**Results**

On the collection date in September 2011, we observed a total of 45 associated species (algae: 13; animals: 32) with an average (±SE) of 14 ± 3 by experimental plot (habitat-forming species excluded). An average total abundance cover of 94 ± 38% (algae: 58%; animals: 37%) for associated species was observed in each experimental plot. Note that total abundance can be over 100% since it represent the sum of all species % cover.

No differences in total abundance, species richness, evenness, or Shannon diversity of the associated species were observed among all treatments (Fig. 8). Also, varying dominance structure and richness in habitat-forming species (HFS), and their identity in the monospecific treatment, did not change the abundance structure (pseudo-$F_{10,45} = 1.20$; $p = 0.2110$) or the composition (data transformed in presence/absence; pseudo-$F_{10,45} = 0.76$; $p = 0.8570$) of associated species. Moreover, our results show

that the colonization in CONT and SHEL treatments did not produce differences in the community properties compared with the presence of any HFS in mono- or polyspecific treatments (Fig. 8). When each of the HFS monospecific treatments was contrasted separately, the Shannon diversity of associated species MYTI is higher than FUED treatments ($t$-ratio = 3.42; $p = 0.0110$). Similar results obtained with biomass (kJ) were analysed (detailed results and figures not shown).

The encrusting algae *Ralfsia clavata* covered up to 80% of the rock surface under the experimental grids in all treatments. This alga rarely covered more than 10% in the natural community. Indeed, when we contrasted *R. clavata* cover between NATU and all other treatments, its percentage cover was marginally different ($p < 0.05$). By removing *R. clavata* from the analyses, the structure within the assemblage in the AHJH treatment became different from the two macroalgal monospecific treatments, FUED ($t$-ratio = 2.20, $p = 0.0210$) and FUVE ($t$-ratio = 1.88, $p = 0.0170$), and became marginally different from the ALJL treatment ($t$-ratio = 1.61, $p = 0.0840$) and MYTI treatment ($t$-ratio = 1.72, $p = 0.0590$) (see Fig. 11 in supporting information section). *Gammarus* spp. and recruits of *Fucus* spp. are the main taxa responsible for the difference between these treatments, respectively explaining up to 33% and 22% of differences. FUED and FUVE have more *Fucus* recruits than AHJH, while the latter has more *Gammarus* spp. and *Mytilus* spp. Analyses of the composition did not show significant results (see Fig. 11).

The separate collection of the organisms that were loosely attached to or caught by the grid (including various sessile organisms that were not attached to habitat-forming species or the ground; e.g. organisms within or on detritus or macrophyte species that were not present in the experimental site tide level) allowed us to remove them from the data set and perform again the same analyses. Without this "grids effect" and *Ralfsia* spp, the structure of associated species in AHJH remained different from FUED and FUVE. The treatments SHEL, CONT. and MYTI showed a

difference in structure with AHJH (t = 2.04, $p = 0.0420$; t = 1.81, $p = 0.0490$ and t = 1.81, $p = 0.0330$ respectively). Moreover, AHJH showed a marginally different assemblage structure from ALJH and ALJL (t = 1.55, $p = 0.0740$ and t = 1.57, $p = 0.0690$ respectively; Fig. 12 in supporting information section). The variability between these treatments is explained by many species, but the two main species responsible for the differences were the gastropods *Lacuna vincta* and *Margarites helicinus*, respectively explaining up to 6% and 4% of differences. The same pattern emerges when analysing the data in kJ.

**Difference in trophic guild**

We first compared the three trophic guilds together among the treatments and no difference in their structure was found (Pseudo-$F_{11,50} = 1.064$; $p = 0.389$; Fig. 9). Second, we analyzed each trophic guild separately and compared them among treatments. We did not observe an effect of richness, evenness, or identity of the HFS on the Grazers (total abundance: $F_{11,50} = 0.92$; $p = 0.5257$ and richness: $F_{11,50} = 1.08$; $p = 0.3978$), Filter feeders (total abundance: $F_{11,50} = 1.12$; $p = 0.3665$ and richness: $F_{11,50} = 1.51$; $p = 0.1571$), and Omnivores (total abundance: $F_{11,50} = 1.33$; $p = 0.2341$ and richness: $F_{11,50} = 0.85$; $p = 0.5925$).

Our results show no significant difference among treatments for the Filter feeders in terms of structure or composition. There was, however, a difference in structure of the Grazers between FUVE, FUED, and SHEL treatments ($t$ =2.25, $p_{mc} = 0.0400$; $t = 2.90$, $p_{mc} = 0.0190$). The omnivores showed differences in structure between some treatments. FUED is different from AHJH ($t = 2.60$; $p_{mc} = 0.0060$), AHJM ($t = 3.23$; $p_{mc} = 0.0050$), and MYTI ($t = 2.51$; $p_{mc} = 0.0230$), and marginally different from FUVE ($t = 1.97$; $p_{mc} = 0.0600$). FUVE is different from AHJH ($t = 2.52$; $p_{mc} = 0.0070$), AHJM ($t = 2.67$; $p_{mc} = 0.0190$), and ALJM ($t = 1.96$; $p_{mc} = 0.0470$).

**Primary production**

All productivity variables (Net primary production: NPP; community Respiration: R; and Gross Primary Production: GPP=NPP+R) included plots with the three manipulated HFS. At the time of the measurement in July 2011, we observed an average (±SE) of $8 \pm 2$ species by experimental plot and an average % cover of $101 \pm 41$ (without HFS: richness = $6 \pm 2$; abundance = $21 \pm 20$. The average richness for algae and animals was $4 \pm 1$. The Spearman correlation (0.63) between the community in July (time of the production measurement) and September (end of the experiment) showed a high similarity, meaning that the community at the time of measurement and at the end of the experiment remained mostly the same. In figure 10, the dotted lines represent the primary production of natural communities (±CI95% of values obtained during July 2010 for 20 natural plots on the same site). For the same area, the natural level of productivity is a little higher than our experimental plots. We consider that this measure gives good estimates of the primary productivity of natural communities during the summer 2011.

The three variables of the primary production measurement were all compared among treatments. MYTI (mussels alone) has the lowest NPP, R, and GPP of all treatments (Fig. 10). The R and GPP showed large differences between the two levels of abundance tested regardless of evenness levels. The two macroalgae have the same R and GPP values level than the high abundance treatments. However, for the NPP some differences occur within the high abundance treatments. The monospecific treatment of FUVE and FUED showed similar NPP. FUED were different compared with all other treatments (except AHJM). FUVE is the same as all other high abundance treatments (except AHJM).

## Discussion

In this paper, we attempted to define the role of richness, evenness, identity, and abundance of habitat-forming species (HFS) on their associated species and community productivity. Generally, our results do not support our hypotheses that predicted a positive effect of the HFS diversity profile (richness, evenness, abundance, identity) on the characteristics of associated species. However, we did observe an effect of HFS richness on the structure of the associated species. Interestingly, all monoculture treatments showed differences in the structure of their grazer and omnivorous guilds but not in filter feeders. The effect of HFS on community functions was solely driven by the abundance of HFS macroalgae that increased community productivity variables.

### Effect of HFS on richness, evenness, identity, and abundance of associated species

In our experiment we did not observe a broad impact of HFS richness, evenness, identity, and abundance on associated species characteristics. We are confident that these non-significant results were not due to the sample size used (n = 4 and 6, see Methods), as *post hoc* power analyses indicated that, depending on a variable considered, a sample size varying between 12 and 305 would have been required to get significant results (detailed analyses not shown). Redundancy between the two *Fucus* species, inherent in the experimental design, would suggest that as long as one species can compensate for the loss or decline of the other, there will be no difference in community processes as theoretically predicted (Naeem et al. 2009). However, mussel and macroalgae treatments (FUED, FUVE, and MYTI) resulted in the same associated species characteristics after 16 weeks of colonization. This was contrary to our expectations because mussels change the heterogeneity of the rocky bottom surface by retaining sand and allowing species like Polychaeta to settle into the mussel bed (Norling and Kautsky 2007). A fully structured soft-bottom community naturally associated with mussel beds may not have had time to become established

during one season, thus explaining why we did not see different assemblages between the macroalgae (FUED and FUVE) and MYTI treatments. Also, the treatment with empty *Mytilus* spp. shells (SHEL) presented a community with characteristics similar to one with living mussels (MYTI). Indeed, by increasing the heterogeneity of the substrate, empty shells do provide refuge for organisms from predation, wave shock, and desiccation, which makes the shell substrate just as important as living mussels (Gutiérrez et al. 2003, Guay and Himmelman 2004).

Our experiment was designed to test potential effects in the mid-low intertidal zone where the macroalgae canopy biomass was maximal, and offers constant optimized protection for understory organisms. It is at this intertidal zone that we usually observe a high diversity of associated fauna (personal observations). The link between HFS diversity and their associated species might have depended upon the tidal level considered (Bertness et al. 1999). Indeed, in the low intertidal zone, biotic factors control the community, while in the high intertidal zone abiotic factors control the community (Menge and Lubchenco 1981, Scrosati et al. 2011). In the high intertidal zone, harsher environmental conditions prevail and the protective influence of habitat-forming species is greater (Watt and Scrosati 2013).

**Effect of HFS on the structure and composition of associated species**

Although we did not observe much effect of the HFS diversity profile on the aggregated characteristics of the associated community, the effects on abundance structure (multivariate) were, however, detected. This was somewhat expected as when assemblages are compared, univariate tests (species independent) are often less sensitive than multivariate ones (species dependent; Warwick and Clarke 1991). In our study, evenness in HFS abundances influenced the structure of the associated species. Indeed, in the AHJH treatment, where the three HFS were present in almost equal proportions, the structure of the associated species was different compared with the three HFS in the monospecific treatments (FUED, FUVE, MYTI). The three main

species responsible for the differences in structure between the monospecific and the polyspecific treatments were *Gammarus* spp., *Mytilus* spp., and *Fucus* recruits. FUED and FUVE have more *Fucus* recruits than AHJH, while the latter has more *Gammarus* spp. and *Mytilus* spp. recruits. The *Gammarus* spp. would prefer the complex environment offered by the polyspecific AHJH treatments since they feed on small invertebrates, worms, small algae, and detritus (Greze 1968), which are probably in greater abundance amongst mussels and protected by the macroalgae against predation and desiccation at low tide (Largaespada et al. 2012). On the other hand, the absence of the whiplash effect (sensu Dayton 1975) from macroalgal fronds in the MYTI treatment would enhance the establishment of new individuals of *Fucus* spp., as seen in our results.

The observed effects on the structure were interesting as they suggest a link with the increased complexity induced by the mussel bed and macroalgae canopy cover present in the AHJH treatment. This difference was not found with our low abundance assemblages and lower evenness (ALJL) among the three HFS. Our results are in accordance with other studies which found an impact of a change in the identity (macroalgae species with morphological difference) of seaweed on structure but not on community characteristics (univariate) of richness and abundance of invertebrate epifauna (Bates and DeWreede 2007).

**Analysis by trophic guilds**

The diversity profile of HFS did not have any effect on the abundance structure in guilds and within each guild separately among all treatments. Nonetheless, the HSF diversity profile affected the abundance structure of both grazers and omnivores, while it did not affect the filter feeders. Since each species offers different functional traits, richness triggers a greater range of functional traits (Danovaro 2012). In our study, changing the structure within a functional group could possibly affect the functions in the community in a longer term. The incorporation of functional group

analyses (as with trophic guilds) in BEF studies increase the chance of identifying potentially key mechanisms that would otherwise be missed with only the analysis of the components of diversity (Petchey and Gaston 2002, Griffin et al. 2009). Our results suggest that if the HFS diversity profiles were modified, as in our treatments, the ability of each functional group (or trophic guild) to carry out their functions (e.g. grazing activity, decomposition, etc.) within the community would be affected. This would be worth to be addressed in a longer term experiment.

**Effect of HFS on primary productivity**

We did not observe an effect of richness or evenness on the productivity values (net primary production: NPP; respiration: R; and gross primary production: GPP) of communities, whereas, theoretically, the values should, increase with producer species richness (Naeem et al. 1996, Hooper and Vitousek 1997). The productivity variables were positively influenced by the total abundance of the two manipulated macroalgae. Indeed, the most abundant treatments that included macroalgae (monospecific FUVE and FUED and polyspecific AH-) had higher values of R and GPP than all of the low abundance treatments (polyspecifics AL-). For the AHJM and AHJL treatments, NPP values were higher than all low abundance treatments except for AHJH. The AHJH treatment had the same NPP as the low abundance treatments; in part, this may be due to the inclusion of a greater proportion of FUVE, which is more associated with lower NPP values (although not statistically significant) than FUED. In this regard, similar responses in productivity between our HFS algae, *Fucus distichus edentatus* and *Fucus vesiculosus*, would additionally support their status as a redundant species in our system. Nevertheless, our results strongly suggest that their high abundance levels in nature are critical for the whole shore productivity.

**Perspectives on biodiversity relationships in the subarctic context**

In our study area, ice-scouring episodes in the spring can partially reset the benthic community (Archambault and Bourget 1983). The succession pattern following such an event implies that the community species richness, abundance, and identity changes throughout the summer (McCook and Chapman 1993). It is possible that the general richness and evenness effect of habitat-forming species (HFS) become more important in a well-established and less disturbed community. This may explain, in part, why our 16-week experiment may not have detected all potential HFS diversity effects.

The link between the diversity of HFS and their associated species is based on species relationships and interactions. The chances of having stronger interactions among species generally increases with diversity (Benedetti-Cecchi 2009). Therefore, the removal of important species can lead to indirect effects with a cascading loss of species through a series of secondary extinctions (Dayton 1975, Grabowski and Kimbro 2005, Lilley and Schiel 2006). These changes in the interactions among species will first influence the structure of the community before an actual species loss or exclusion takes place. This might be the reason why we detected effects on abundance (multivariate) structures but not on richness or total abundance. In their review, Hillebrand et al. (2008) predicted that a change in dominance would occur before loss of species with consequences in abundance structure (dominance/evenness), species interactions, and community processes within the ecosystems. Our results showed that these structural changes within abundant species would not have much effect on short-term species establishment. Further investigations at larger scales (site and regional scale) are needed to better predict large changes within assemblages. However, manipulative studies are difficult or impossible at larger scales. Indeed, most manipulative studies have been done at a limited spatial scale (e.g. meter-scale Crowe et al. 2013) and temporal consequences of the diversity effect may either be seen only after a few years, but also the effect

may be greater or null thereafter (Stachowicz et al. 2008). Our observed HFS richness effect on some abundance structures of the newly established community may just be an indication that the effects of the HFS diversity profile generate complex responses within the associated community. Consequently, longer experiments would have helped to understand further diversity interactions. But, in the subarctic environment studied, this was not possible due to macroalgal senescence, very harsh autumn conditions, and ice cover in winter. Also, small differences in proportional densities of HSF among our polyspecific treatments (see Table 3) may have slightly affected our analyses. Additional tests with varying assemblages within levels of abundances/evenness could be evaluated in future to gain insight to this potential effect. Further extension of such *in situ* manipulative studies to higher intertidal levels where environmental conditions are more hasher (as previously discussed above), and other marine habitats, would certainly add to our understanding of the role of habitat-forming species in maintaining local biodiversity levels. Nevertheless, the linkage of biodiversity with ecosystem function must also be understood in environmentally driven habitats. The strength of the compensatory dynamics that influence community stability varies with latitude. Compensatory dynamics within assemblages can also be influenced by the HFS as they control the associated species (Bulleri et al. 2012). Moreover, the canopy removal effect on community stability is a function of latitude and environmental forcing (Campbell et al. 2011, Bulleri et al. 2012).

Our study demonstrate the need for *in situ* experiments that reflect real-life interactions among species is crucial in order to better assess the role of biodiversity on ecosystem functioning and the potential effect of species abundance structures changes on their community functions.

## Concluding remarks

In this work, the effects of richness, evenness, identity, and abundance of habitat-forming species (HFS) on the diversity and establishment of associated species were studied over a 16-week period in a subarctic environment. There was an effect of the HFS richness and evenness on the abundance structure of the associated species but not on their aggregative community characteristics (richness, total abundance, diversity, etc.). These results support the idea that local loss of a HFS would first promote changes in the abundance structure before changes in the composition community, including species extinction. Moreover, the study of the richness effect alone in biodiversity/ecosystem functioning studies would only focus on one important, but incomplete, component of biodiversity. Richness effect studies, when coupled with other aspects of diversity such as evenness, allow the exploration of the effect of different mechanisms on community processes. To our knowledge, our *in situ* study in a subarctic environment is one of the first to examine the effects of richness, evenness, identity and abundance of habitat-forming species on associated community structure and productivity. This research represents a step forward to a better understanding of the general effect of biodiversity on community dynamics.

## Acknowledgements

We thank S. Cimon, P. Carrier-Corbeil, M. Gagnon, D-A Gauthier, L. Joseph, S. Lavoie, W. H. Landry and H. Perelman for their precious help in the field and laboratory. We also thank Drs. C. Golléty and D. Davoult for fruitful discussions on productivity measures. Special thanks to Dr. A. Lazartigues for helpful comments on earlier versions of the manuscript. We thank two anonymous reviewers for providing constructive comments and criticisms on the final version. This study is part of J.L.'s Ph.D. dissertation at UQAC. This project is a contribution to the research program of Québec-Océan. Financial support was provided by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants) and FQRNT (Quebec Funds for Research in Nature and Technology, New University Researchers Start-up Program) to M.C.

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Table 2 : Composition of all treatments including the six artificial polyspecific and three monospecific communities for the three manipulated habitat-forming species: *Fucus distichus edentatus*, *Fucus vesiculosus* and *Mytilus* spp. The percentage covers that were used to create the three levels of evenness and two levels of abundance including information on the procedural controls (empty shells and grid) are shown. See methods section for details.

| Note | Treatment name | Abundance (A) | Evenness (J) | *Fucus distichus edentatus* (% cover) | *Fucus vesiculosus* (% cover) | *Mytilus* spp. (% cover) |
|---|---|---|---|---|---|---|
| Plurispecific | AHJH | High | High | 50 | 50 | 30 |
| Plurispecific | AHJM | High | Medium | 80 | 30 | 15 |
| Plurispecific | AHJL | High | Low | 85 | 15 | 5 |
| Plurispecific | ALJH | Low | High | 20 | 15 | 15 |
| Plurispecific | ALJM | Low | Medium | 30 | 5 | 10 |
| Plurispecific | ALJL | Low | Low | 40 | 5 | 5 |
| Monospecific | FUED | | | 100 | 0 | 0 |
| Monospecific | FUVE | | | 0 | 100 | 0 |
| Monospecific | MYTI | | | 0 | 0 | 30 |
| Empty mussel shells only | SHEL | | | 0 | 0 | 30 |
| Only grid | CONT | | | 0 | 0 | 0 |
| Natural community* | NATU | | | | | |

*percentage covers of the three habitat-forming species were not manipulated

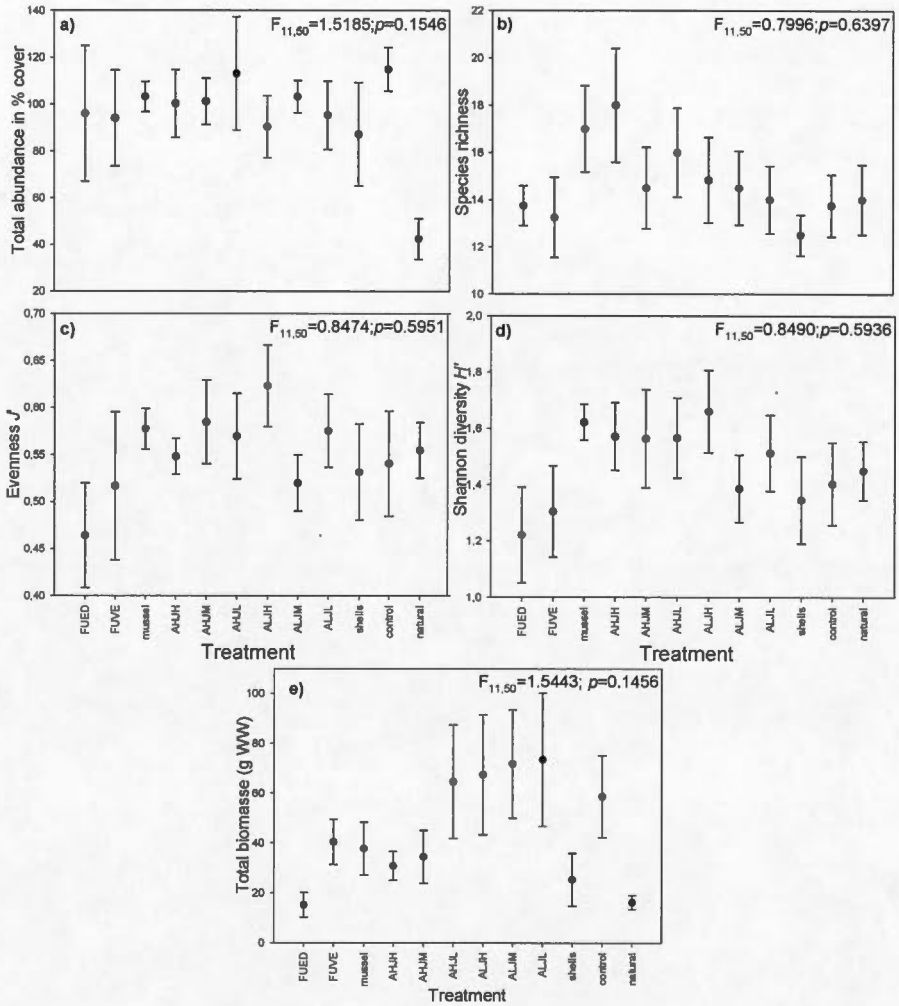


**Figure 7 :** Average values (±SE) of a) total abundance (% cover), b) species richness, c) evenness (Pielou *J'*), and d) diversity index (Shannon *H'*) e) in total abundance in biomass (g of Wet Weight) of associated species for each treatment. Treatments consisted of artificial assemblages with habitat-forming species having 2 levels of abundance (high, AH: 100-130 total % cover; and low, AL: 40-45% cover) and three levels of evenness *J'* values (high ±0.097: JH; medium ±0.75: JM; and low ±0.55: JL) as well as monoculture treatments with 100% cover of *Fucus distichus edentatus* (FUED), 100% cover of *Fucus vesiculosus* (FUVE), 30% *Mytilus* spp. (mussel), and a control with 30% *Mytilus* spp. empty shells (shells) and a natural reference community (natural). Percentage cover data set was used here, see Methods section.

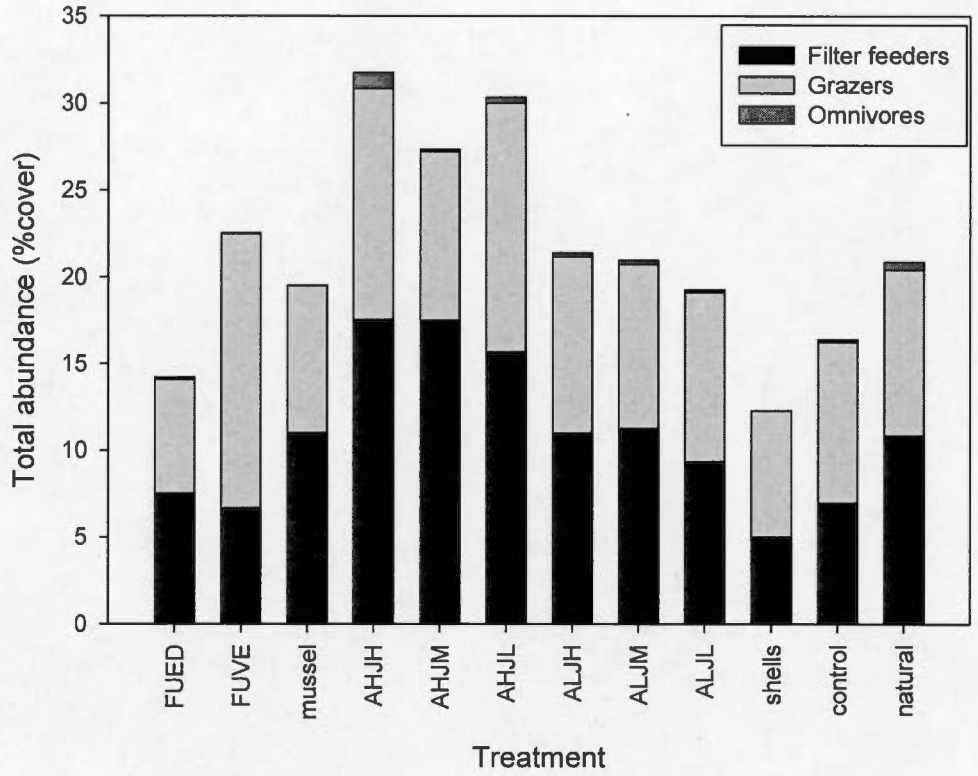


**Figure 8 :** Distribution of total abundance in percentage cover of three trophic guilds among treatments: Grazers (8 species), Filter feeder (5 species) and Omnivores (11 species). See Table 1 for the details of the treatments and Table S1 in supporting information section for details of the trophic guilds group composition.

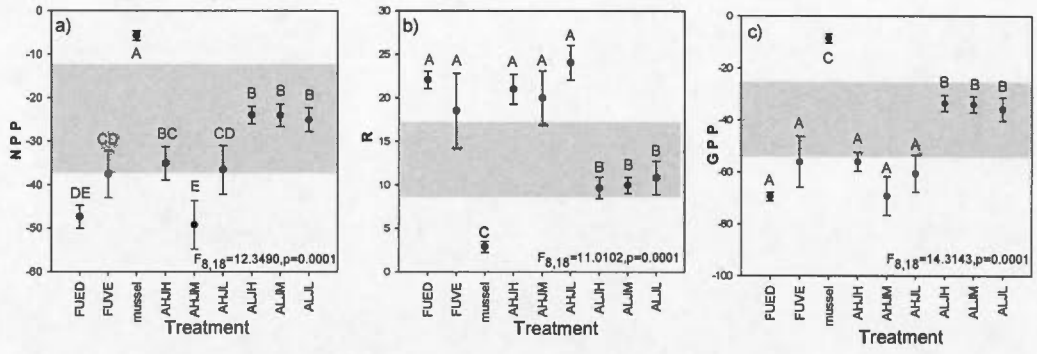


**Figure 9 :** Average (±SE) values of productivity variables ($\mu molCO_2*mlO_2^{-1}*min^{-1}$) of a) Net primary production (NPP), b) community respiration (R) and the c) gross primary production (GPP). Measurements were taken in July 2011 from each treatment and from 3 randomly chosen replicates (see Methods). The dotted lines represent the confidence interval (±95%) of the production done on natural community (see results section for details). Levels not connected by the same letter are significantly different. See Table 3 for the details of the treatment.

## Supporting information

Table 3 : Taxa list of all observed organisms at the end of the experiment (September 2011). For the animals, trophic guilds in which they were classified are shown.

| Algae | Species name | Phylum | Class | Order | Family | Genus | Species |
|---|---|---|---|---|---|---|---|
| **Brown algae** | *Fucus distichus* | Phaeophyta | Phaeophyceae | Fucales | Fucaceae | *Fucus distichus* | *Edentatus* |
| | *Fucus vesiculosus* | Phaeophyta | Phaeophyceae | Fucales | Fucaceae | *Fucus* | *Vesiculosus* |
| | *Ascophyllum* | Phaeophyta | Phaeophyceae | Fucales | Fucaceae | *Ascophyllum* | *Nodosum* |
| | *Chordaria* | Phaeophyta | Phaeophyceae | Ectocarpales | Chordariaceae | *Chordia* | *Flagelliformis* |
| | *Ectocarpus spp.* | Phaeophyta | Phaeophyceae | Ectocarpales | Ectocarpaceae | *Ectocarpus* | |
| | *Ralfsia fungiformis* | Phaeophyta | Phaeophyceae | Ectocarpales | Ralfsiaceae | *Ralfsia* | *Fungiformis* |
| | *Ralfsia clavata* | Phaeophyta | Phaeophyceae | Ectocarpales | Ralfsiaceae | *Ralfsia* | *Clavata* |
| | *Scytosiphon* | Phaeophyta | Phaeophyceae | Scytosiphonales | Scytosiphonaceae | *Scytosiphon* | *Lomentaria* |
| | *Petalonia fascia* | Phaeophyta | Phaeophyceae | Scytosiphonales | Scytosiphonaceae | *Petalonia* | *Fascia* |
| **Red algea** | *Hildenbrandia* | Rhodophyta | Rhodophyceae | Cryptonemiales | Hildenbrandiaceae | *Hildenbrandia* | *Prototypus* |
| | *Porphyra spp.* | Rhodophyta | Rhodophyceae | Bangiales | Bangiaceae | *Porphyra* | |
| | *Clathromorphum circumscriptum* | Rhodophyta | Rhodophyceae | Corallinales | Corallinaceae | *Clathromorphum* | *Circumscriptum* |
| | *Rhodomela* | Rhodophyta | Rhodophycaea | Ceramiales | Rhodomelaceae | *Rhodomela* | *Confervoides* |
| | *Polysiphonia spp.* | Rhodophyta | Rhodophyceae | Ceramiales | Rhodomelaceae | *Polysiphonia* | |
| **Green algae** | *Ulvaceae* | Chlorophyta | Chlorophyceae | Ulotrichales | Ulvaceae | | |
| | *Ulothrix sp.* | Chlorophyta | Chlorophyceae | Ulotrichales | Ulotrichaceae | *Ulothrix* | |
| **Trophic guild** | | | | | | | |
| **Filter feeders** | *Aulactinia stella* | Cnidaria | Anthozoa | Actiniaria | Actiniidae | Aulactinia | Stella |
| | *Macoma Baltica* | Mollusca | Bivalvia | Veneroida | Tellinidae | Macoma | Baltica |
| | *Mytillus edulis* | Mollusca | Bivalvia | Filibranchia | Mytilidées | Mytillus | Edulis |
| | *Mya arenaria* | Mollusca | Bivalvia | Myoida | Myidae | Mya | Arenaria |
| | *Skeneopsis* | Mollusca | Gastropoda | Neogastropoda | Skeneosidae | Skeneopsis | Planorbis |
| | *Pectinaria gouldii* | Annelida | Polychaeta | Canalipalpata | Pectinariidae | Pectinaria | Gouldii |
| | *Balanus crenatus* | Arthropoda | Maxillopoda | Sessilia | Balanidae | Balanus | Crenatus |
| | *Semibalanus* | Arthropoda | Maxillopoda | Sessilia | Archaeobalanidae | Semibalanus | Balanoides |
| **Grazers** | *Littorina obtusata* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae | Littorina | Obtusata |
| | *Littorina saxatilis* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae | Littorina | Saxatilis |
| | *Littorina littorea* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae | Littorina | Littorea |
| | *Lacuna vincta* | Mollusca | Gastropoda | Neotaenioglossa | Littorinidae | Lacuna | Vincta |
| | *Margarites* | Mollusca | Gastropoda | Archaeogastropoda | Trochidae | Margarites | Helicinus |
| | *Tectura* | Mollusca | Gastropoda | Patellogastropoda | Lottidae | Tectura | Testudinalis |
| | *Jaera marina* | Arthropoda | Malacostraca | Isopoda | Janiridae | Jaera | Marina |
| **Omnivores** | *Nucella lapillus* | Mollusca | Gastropoda | Neogastropoda | Muricidae | Nucella | Lapillus |
| | Sipuncula | Sipuncula | Sipunculidea | | | | |
| | Oligochaeta | Annelida | Clitellata | | | | |
| | Polychaeta | Annelida | Polychaeta | | | | |
| | *Nereis* spp. | Annelida | Polychaeta | Aciculata | Nereididae | Nereis | |
| | *Eteone longa* | Annelida | Polychaeta | Aciculata | Phyllodocidae | Eteone | Longa |
| | *Fabricia sabella* | Annelida | Polychaeta | Canalipalpata | Sabellidae | Fabricia | Sabella |
| | *Sabellaria* | Annelida | Polychaeta | Canalipalpata | Sabellidae | | |
| | *Polydora* spp. | Annelida | Polychaeta | Canalipalpata | spionidae | Polydora | |
| | *Polynoidae* spp. | Annelida | Polychaeta | Aciculata | Polynoidae | | |
| | *Lepidonotu* | Annelida | Polychaeta | Aciculata | Polynoidae | Lepidonotus | squamatus |
| | *Phyllodocidae spp.* | Annelida | Polychaeta | Aciculata | Phyllodocidae | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | *Capitellidae* | Annelida | Polychaeta | | | | |
| | *Gammarus* spp. | Arthropoda | Malacostraca | Amphipoda | | | |
| | *Cancer irroratus* | Arthopodes | Malacostraca | Decapoda | Cancridae | Cancer | irroratus |

Table 4 : Average (±SE) of percentage cover for each taxa in all treatments. Note that for some species, only identification at the genus level (or above) was possible since most of the individual were recruits.

| Treatments | AHJH | | AHJM | | AHJL | | ALJH | | ALJM | | ALJL | | FUED | | FUVE | | MYTI | | SHEL | | CONT | | NATU | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE | mean | ±SE |
| **Macroalgea** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Fucus* spp | 3.10 | 4.00 | 6.45 | 7.00 | 21.27 | 16.67 | 14.95 | 16.17 | 8.75 | 8.83 | 22.03 | 21.83 | 14.45 | 18.75 | 8.69 | 9.25 | 9.54 | 13.75 | 4.24 | 15.00 | 18.10 | 29.75 | | |
| *Ascophyllum nodosum* | | | | | | | 1.22 | 0.50 | | | | | | | | | | | | | 5.00 | 2.50 | | |
| *Laminaria* spp | | | | | 0.41 | 0.17 | 2.04 | 0.83 | | | | | | | | | | | 0.50 | 0.25 | | | | |
| **Ephemeral algae** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Enteromorpha* spp | | | | | | | 0.41 | 0.17 | | | | | | | | | | | | | | | | |
| *Antithamnion* spp | 0.05 | 0.03 | 0.82 | 0.33 | | | | | | | | | | | | | | | | | | | | |
| *Chordaria flagelliformis* | 1.55 | 1.00 | 1.22 | 0.50 | 3.21 | 2.50 | 3.60 | 1.83 | 0.82 | 0.33 | 1.67 | 1.00 | 15.50 | 7.75 | 0.75 | 0.38 | 3.00 | 1.50 | 2.31 | 2.00 | 2.87 | 1.75 | | |
| *Porphyra* spp | 0.84 | 0.50 | 2.81 | 1.50 | 1.33 | 1.17 | 6.69 | 4.00 | 1.03 | 0.67 | 8.76 | 6.67 | 0.48 | 0.38 | | | 4.50 | 3.75 | 0.50 | 0.25 | 1.00 | 0.50 | 4.08 | 1.67 |
| *Rhodomela confervoides* | 1.17 | 0.75 | | | | | 1.20 | 0.58 | 1.60 | 0.75 | | | | | | | | | | | 0.25 | 0.13 | | |
| *Ulvaceae* | 2.58 | 2.33 | 3.49 | 2.17 | 2.11 | 1.42 | 1.97 | 1.50 | 0.42 | 0.25 | | | | | | | 1.44 | 0.88 | 0.95 | 0.63 | 1.80 | 1.38 | | |
| **Encrusting algae** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Clathromorphum circumscriptum* | | | 1.22 | 0.50 | | | | | | | | | | | | | | | | | | | <0.00 | <0.00 |
| *Hildenbrandia prototypus* | | | | | | | <0.00 | <0.00 | | | | | | | | | | | | | | | <0.00 | <0.00 |
| *Ralfsia clavata* | 25.70 | 34.42 | 6.59 | 44.33 | 28.34 | 43.00 | 10.34 | 28.17 | 10.41 | 50.67 | 23.14 | 35.33 | 42.08 | 59.25 | 37.17 | 53.75 | 5.48 | 47.00 | 31.61 | 46.25 | 28.10 | 51.50 | 10.81 | 9.00 |
| *Ralfsia fungiformis* | | | | | | | | | | | | | | | | | | | | | | | 0.20 | 0.08 |
| **Grazers** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Gammarus* spp | 12.25 | 25.00 | 11.75 | 16.96 | 11.97 | 17.42 | 14.05 | 14.79 | 12.03 | 20.29 | 14.98 | 10.71 | 1.80 | 3.19 | 3.14 | 7.75 | 9.74 | 16.31 | 13.66 | 10.13 | 12.61 | 10.81 | 11.51 | 10.02 |
| *Jaera marina* | 0.24 | 0.58 | 0.25 | 0.40 | 0.21 | 0.26 | 0.17 | 0.39 | 0.20 | 0.33 | 0.21 | 0.26 | 0.02 | 0.03 | 0.11 | 0.10 | 0.39 | 0.55 | 0.10 | 0.11 | 0.11 | 0.11 | 0.22 | 0.35 |
| *Lacuna vincta* | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | 0.02 | 0.01 | <0.00 | <0.00 | 0.01 | 0.01 | 0.04 | 0.03 | 0.01 | <0.00 | 0.01 | <0.00 | 0.01 | <0.00 | <0.00 | <0.00 |
| *Littorina littorea* | 0.01 | <0.00 | | | | | | | | | 0.01 | 0.01 | | | | | | | | | | | | |
| *Littorina obtusata* | 6.18 | 8.27 | 2.78 | 5.67 | 5.76 | 9.21 | 3.38 | 5.21 | 3.41 | 5.01 | 4.57 | 5.48 | 2.33 | 3.79 | 5.43 | 11.58 | 0.57 | 3.27 | 3.18 | 3.56 | 4.03 | 4.88 | 2.98 | 6.04 |
| *Littorina saxatilis* | 2.28 | 4.36 | 1.03 | 3.46 | 2.19 | 4.80 | 2.46 | 4.52 | 2.12 | 4.03 | 2.87 | 3.98 | 1.61 | 2.75 | 1.57 | 4.06 | 0.83 | 4.45 | 2.89 | 3.48 | 3.17 | 4.31 | 1.15 | 3.11 |
| *Margarites helicinus* | 0.09 | 0.05 | 0.39 | 0.18 | 0.07 | 0.05 | 0.05 | 0.04 | 0.17 | 0.10 | 0.04 | 0.02 | | | 0.11 | 0.06 | 0.17 | 0.22 | 0.18 | 0.09 | | | 0.15 | 0.07 |
| *Tectura testudinalis* | 0.02 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | <0.00 | <0.00 | <0.00 | 0.01 | 0.01 | | | 0.01 | <0.00 | 0.01 | 0.01 | 0.03 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 |
| **Filter feeders** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Macoma Baltica* | 0.01 | 0.01 | | | | | | | 0.01 | 0.01 | 0.01 | <0.00 | 0.01 | 0.01 | 0.02 | 0.01 | 0.02 | 0.01 | | | | | | |
| *Mya arenaria* | | | 0.02 | 0.01 | | | | | | | | | | | | | | | | | | | <0.00 | <0.00 |
| *Mytilus* spp | 11.25 | 15.18 | 9.31 | 13.24 | 12.08 | 12.07 | 8.53 | 10.48 | 8.77 | 10.80 | 4.52 | 6.73 | 5.86 | 5.22 | 2.19 | 5.66 | 4.52 | 10.24 | 3.05 | 2.64 | 3.61 | 3.39 | 9.19 | 10.82 |
| *Balanus* spp | 2.27 | 2.34 | 4.66 | 4.26 | 6.26 | 3.59 | 0.45 | 0.50 | 0.78 | 0.46 | 3.90 | 2.63 | 3.81 | 2.29 | 0.82 | 1.00 | 0.29 | 0.76 | 3.78 | 2.38 | 4.30 | 3.58 | 0.01 | <0.00 |
| *Pectinaria gouldii* | 0.01 | 0.01 | | | | | | | | | <0.00 | <0.00 | | | | | | | | | | | 0.01 | 0.01 |
| *Skeneopsis planorbis* | 0.01 | 0.01 | <0.00 | <0.00 | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 | <0.00 | 0.01 | <0.00 | | | 0.01 | <0.00 | 0.01 | <0.00 | 0.03 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 |
| **Omnivores** | | | | | | | | | | | | | | | | | | | | | | | | |
| *Oligochaeta* | 0.01 | 0.01 | 0.02 | 0.01 | 0.04 | 0.03 | 0.02 | 0.01 | 0.01 | 0.01 | 0.02 | 0.02 | 0.01 | 0.02 | 0.03 | 0.03 | 0.01 | 0.01 | | | 0.03 | 0.02 | 0.19 | 0.18 |
| *Polychaeta* | | | | | | | | | <0.00 | <0.00 | | | 0.01 | <0.00 | | | | | 0.02 | 0.01 | | | | |
| *Acaria* | 0.02 | 0.01 | 0.07 | 0.03 | 0.10 | 0.07 | 0.02 | 0.01 | 0.01 | 0.01 | <0.00 | <0.00 | 0.03 | 0.02 | 0.06 | 0.04 | 0.01 | 0.01 | | | | | <0.00 | <0.00 |
| *Aulactinia stella* | 0.01 | <0.00 | <0.00 | <0.00 | | | | | | | | | | | | | | | | | | | <0.00 | <0.00 |
| *Capitellidae* | | | <0.00 | <0.00 | | | | | 0.01 | <0.00 | | | | | | | 0.02 | 0.01 | | | | | | |
| *Chironomidea larva* | 0.03 | 0.01 | 0.01 | 0.01 | 0.01 | 0.01 | | | 0.12 | 0.05 | 0.02 | 0.01 | 0.04 | 0.02 | 0.01 | <0.00 | 0.01 | <0.00 | 0.03 | 0.01 | | | 0.04 | 0.02 |
| *Eteone longa* | | | | | | | | | | | 0.01 | <0.00 | | | | | | | | | | | 0.01 | 0.01 |
| *Fabricia sabella* | 0.01 | 0.01 | | | 0.01 | <0.00 | 0.04 | 0.02 | | | 0.01 | <0.00 | | | 0.03 | 0.02 | 0.01 | 0.01 | | | | | 0.10 | 0.09 |
| *Foraminifera* | 0.25 | 0.27 | 0.25 | 0.32 | 0.23 | 0.23 | 0.25 | 0.27 | 0.24 | 0.30 | 0.26 | 0.33 | 0.04 | 0.04 | 0.24 | 0.14 | 0.24 | 0.38 | 0.26 | 0.28 | 0.05 | 0.04 | 0.17 | 0.41 |
| *Lepidonotu squamatus* | 0.02 | 0.01 | | | 0.01 | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 | <0.00 | <0.00 | | | | | 0.01 | 0.01 | | | 0.01 | <0.00 | 0.04 | 0.02 |
| *Nereis* spp | 1.80 | 0.92 | 0.14 | 0.13 | 0.58 | 0.33 | 0.25 | 0.21 | 0.40 | 0.21 | 0.21 | 0.13 | 0.14 | 0.13 | | | | | | | 0.25 | 0.13 | 0.38 | 0.33 |
| *Phyllodocidae* spp | | | | | | | | | | | | | | | | | | | | | | | <0.00 | <0.00 |
| *Plathelminth* | 0.09 | 0.11 | 0.13 | 0.09 | 0.06 | 0.06 | 0.20 | 0.11 | 0.08 | 0.07 | 0.08 | 0.07 | 0.04 | 0.12 | 0.08 | 0.12 | 0.08 | 0.09 | 0.05 | 0.04 | 0.14 | 0.09 | 0.04 | 0.02 |
| *Polydora* spp | 0.01 | <0.00 | | | | | | | | | | | | | 0.01 | <0.00 | | | | | | | <0.00 | <0.00 |
| *Polynoidae* spp | | | <0.00 | <0.00 | | | | | | | <0.00 | <0.00 | | | | | | | | | | | <0.00 | <0.00 |
| *Sabellaria* spp | | | | | | | | | | | | | | | | | | | | | | | <0.00 | <0.00 |
| *Sipuncula* | 0.03 | 0.02 | 0.07 | 0.07 | 0.03 | 0.02 | 0.05 | 0.03 | 0.02 | 0.01 | 0.02 | 0.02 | 0.03 | 0.02 | 0.07 | 0.04 | 0.03 | 0.06 | 0.02 | 0.02 | 0.02 | 0.04 | 0.02 | 0.01 |

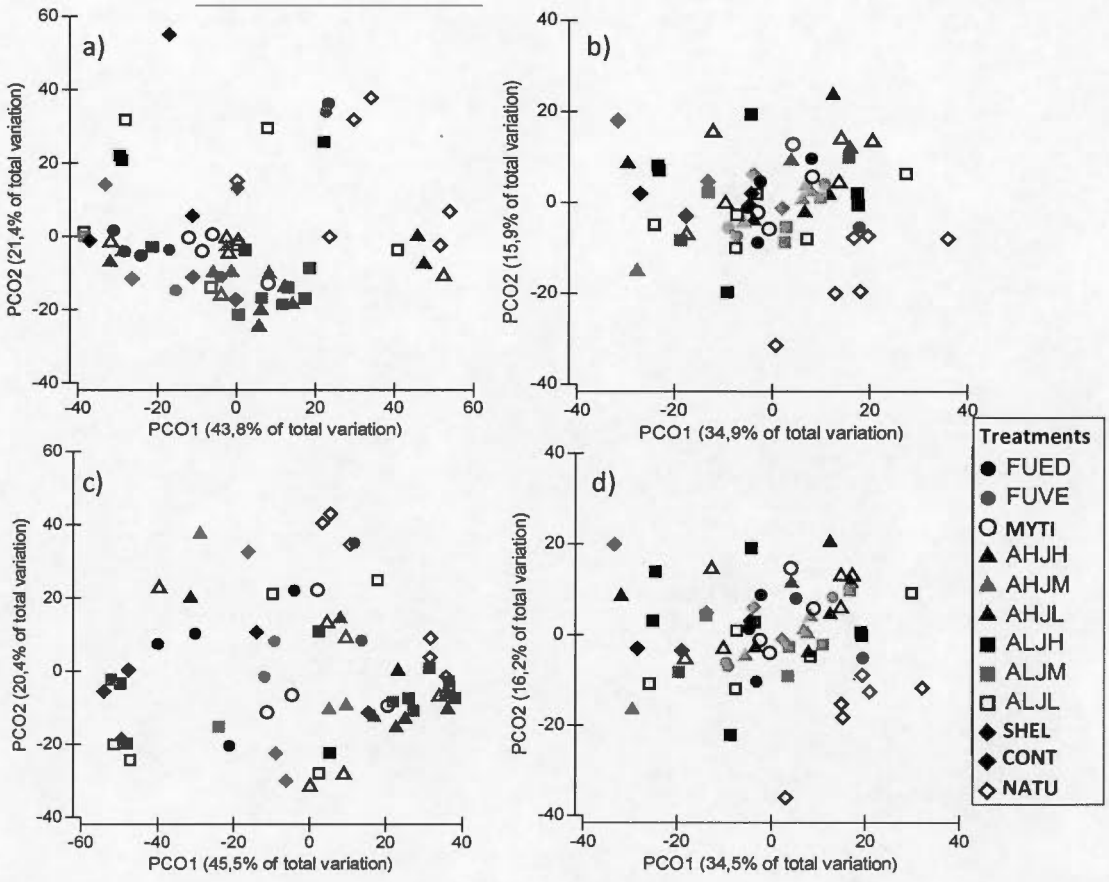


Figure 10 : Percentage cover data set: PCO (Bray Curtis similarity) showing the difference in a) structure and b) composition and without *Ralfsia Clavata* in c) structure and d) composition of the associated species among treatments. See figure 1 in article for details on the treatments.

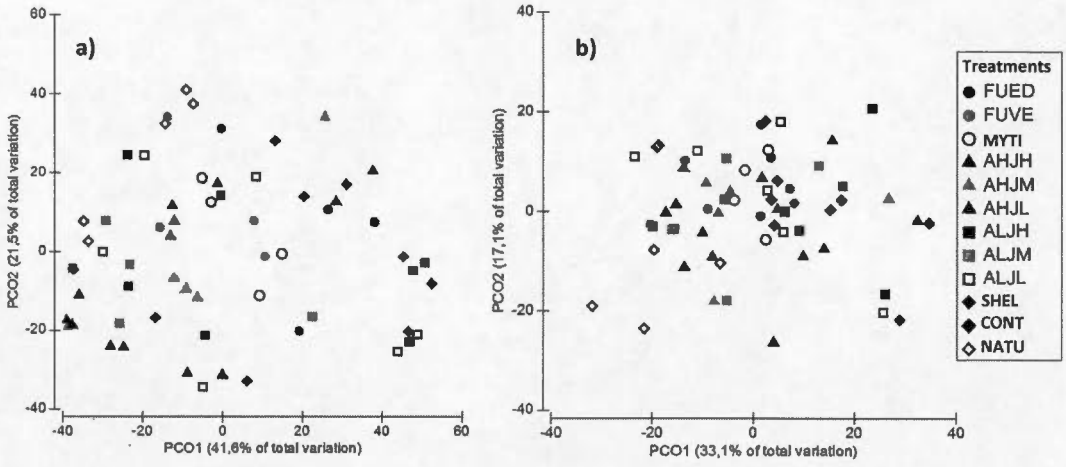


**Figure 11 :** Percentage cover data set without the grid effect: PCO (Bray Curtis similarity) showing differences in a) structure and b) composition. The encrusting species *Ralfsia Clavata* is not included in the analysis. See figure 8 in article for details on the treatments.

# CHAPITRE 4: VOLET 3
# PRODUCTIVITÉ

# BIODIVERSITY COMPONENT EFFECTS ON MACROALGAL PRIMARY PRODUCTIVITY

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## Abstract

Existing rates of species' loss has increased interest in understanding how biodiversity affects ecosystem functioning. Ecosystem productivity is one of the critical functions that may be affected by biodiversity loss, although as of yet, no clear links between ecosystem productivity and diversity profiles have been established. The objective of this study was to define the relationship between macroalgal diversity profiles (as richness, evenness, identity and abundance) and primary productivity within a subarctic intertidal macroalgal community. We used two canopy species (*Fucus* spp.) and four of their associated subcanopy species to build realistic assemblages having four different levels of richness, two levels of evenness and five levels of abundance. The productivity variables of respiration (R), net (NPP) and gross primary productivity (GPP) of these assemblages were measured in mesocosms (0.09 $m^2$). As expected, our results showed a strong positive effect of biomass abundance on all productivity variables while the rates of productivity per gram of algae were slightly lower at the highest abundance levels (600 g). The log response ratio from contrasted treatments showed that richness at high evenness levels had a positive effect on NPP, R and GPP values. Richness at low evenness levels (e.g. assemblages having a dominant algal species) had a positive effect on respiration only. Within the species-rich assemblages (six species), high evenness promoted NPP and GPP except at the lowest abundance level (50 g). The identity effect of the macroalgae on productivity was variable for most monoculture species. Our results illustrate separate and synergetic (overyielding) effects of diversity components (richness, evenness) on productivity. We suggest that the observed overyielding occurred due to complementarity mechanisms, such as light use. Our findings suggest that diversity within macroalgal communities is desirable in order to maintain an efficient use of resources and high productivity within intertidal ecosystems.

**Keywords:** macroalgae, richness, evenness, identity, primary productivity, respiration, complementary effect, overyielding

## Introduction

The rate of species extinction has increased significantly over the past decades (Chapin III et al. 2000, Hooper et al. 2012) to a degree that we might now be witnessing a sixth great geological mass extinction (Barnosky et al. 2011). There are a growing number of studies that have shown that biodiversity has a net positive effect on many ecosystem functions (reviewed in Balvanera et al. 2006, Cardinale et al. 2011). As these functions (e.g. respiration, decomposition, biomass production, etc.) are essential for ecosystem health as well as the maintenance of various services to humans (e.g. depuration, fisheries, etc. Naeem et al. 1995), the need for understanding the links between biodiversity and ecosystem functioning has become important (Chapin III et al. 2000, Hooper et al. 2012). Recent studies have shown that, relative to richer communities, species-poor communities generally capture fewer resources and are marked by lower standing stocks (Hooper et al. 2005, Cardinale et al. 2006) or primary productivity levels (Hector et al. 1999, Hector et al. 2002, Power and Cardinale 2009).

Most studies on biodiversity and ecosystem functioning have been conducted within terrestrial environments (Hector et al. 1999, Tilman et al. 2001, Grace et al. 2007, Isbell et al. 2009, Reich et al. 2012) and it remains unclear if the results from terrestrial studies may be transposed onto marine ecosystems (Stachowicz et al. 2008). Marine ecosystems are among the most productive on Earth and they contain the largest proportion of the Earth's primary productivity (Häder and Figueroa 1997, Falkowski et al. 1998). Within coastal habitats, macroalgae are important producers (John 1971, Häder and Figueroa 1997) and their contribution to benthic community dynamics is essential (John 1971, Charpy-Roubaud and Sournia 1990, Migné et al. 2004, Duarte et al. 2005). However, studies assessing the impact of changes in macroalgal diversity on primary productivity as well as research determining the specific role of habitat forming species (e.g. macroalgal canopy species) on the carbon budget within these marine habitats remain relatively rare (Duarte et al. 2005, Golléty et al. 2008, Power and Cardinale 2009).

Species richness and evenness are the two main components of diversity. Previous studies have shown them to have distinct effects on ecosystem functioning (Nijs and Roy 2000, Wilsey et al. 2005, Cusson et al. 2014, Lemieux and Cusson 2014). Different mechanisms have been proposed

to explain the positive effect of diversity on community functioning (Doak et al. 1998, Loreau and Mazancourt 2008, Isbell et al. 2009). Among these mechanisms, complementarity is one of the most commonly proposed. Richness will positively affect functioning through niche partitioning thereby leading to complementarity among species (Tilman 1999, Stachowicz et al. 2007). Increased richness results in a greater range of species traits within the community. As such, more niches are able to be exploited thereby inducing a greater efficiency of resource use (Hector et al. 2002). As such, complementarity can be detected when an individual species average performance is higher in polyculture than in monoculture (Loreau 2000, Loreau and Hector 2001).

As an important component of diversity, evenness can be a key factor in promoting or maintaining community functioning over time (Stirling and Brian Wilsey 2001, Kirwan et al. 2007, Hillebrand et al. 2008). Similar to richness, evenness has a positive effect on community production as it increases the representation of several highly productive species (Nijs and Roy 2000). On the other hand, low evenness (or high dominance) may dampen the richness effect through a control on resource availability as well as other functions including nutrient flux and net production within the community (Eriksson et al. 2006b, Hillebrand et al. 2008).

The identity effect can be described as a measurement of species specific productivity and an understanding of the unique response of individual species to their environment. Species identity may then be used to predict the strength of the correlation between diversity and productivity. It has been shown that species identity within an assemblage may play an even greater role than richness or evenness on community functioning (Bruno et al. 2005). Changes in species composition alter the distribution of functional traits within the community (Díaz and Cabido 2001, Bruno et al. 2005) affecting both the efficiency of all ecosystem processes and the primary productivity (Hooper and Vitousek 1997, Olabarria et al. 2013).

The particular species present within a community can also affect ecosystem properties by changing the trophic interactions among species (Downing and Leibold 2002). In short, the specific species within a given community can determine which functional traits are available,

while richness defines the range of trait variability and evenness influences the distribution of these traits within the community (Tilman 1997, Loreau 2000, Polley et al. 2003).

The objective of this study is to untangle the role of the components of diversity (richness, evenness, identity and abundance) within a subarctic macroalgal community and then test their respective effects on productivity. In this mesocosm-based study, we determined primary productivity through net primary productivity, respiration and gross primary productivity, from realistic macroalgal assemblages characterized by various diversity profiles within monocultures and polycultures. We used two canopy species and four associated subcanopy species, all occurring naturally together, from a subarctic intertidal environment. We expected different species to have produce differing effects (identity effect), and we hypothesized that a greater richness would promote higher primary productivity (overyielding). Low evenness within a species assemblage should dampen this relationship with the dominance of a specific trait. To our knowledge, this is one of the first studies in a subarctic environment that attempts to unravel the links between the diversity profiles of macroalgae and primary productivity. This study should provide valuable information in regards to the various roles of diversity components on primary productivity and potential existence of overyielding in this marine ecosystem.

## Methods

### Collection of the macroalgae

In order to create macroalgal assemblages having various diversity profiles, we selected common abundant macroalgal species occurring naturally together in the mid-low intertidal zone (48°37′42.5″ N, 68°11′55.7″ W) of the St. Lawrence Estuary, near the municipality of Sainte-Flavie (Quebec, Canada). Two habitat-forming canopy species, *Fucus distichus edentatus* and *F. vesiculosus* as well as four understory macroalgal species, *Chordaria flagelliformis*, Ulvaceae spp., *Porphyra spp.* and *Ceramium rubrum* were harvested in August 2012. The same species (with the exception of *C. rubrum*) were again harvested in July 2013. The algae were placed in cool boxes and promptly transported to the laboratory (located two kilometres from the harvest site). All individual plants were gently handwashed in filtered saltwater in order to remove all visible epibionts. The macroalgae were towel-dried and weighed (± 0.005 g) and then randomly

placed in predetermined and replicated (n = 3) assemblages (see below) within loose mesh tissue bags in an 800 L water tank. The tank reflected the conditions at the harvest site having constant circulation (a rate of flow within the tank of 12.5-15 L/min and a water renewal rate 15-20 L/min) of filtered seawater through silica sand (0.8-1.2 mm Ø with an effective filtration of 20-40 µm), water temperature between 8-12°C and a salinity between 18 and 23 PSI. Light conditions mimicked external light conditions (11h of daylight, 13h of darkness) and emitted wavelengths optimized for absorption by chlorophyll pigments (*a* and *b*) for photosynthesis (fluorescent GRO-LUX lighting having a wide spectrum light 3600K and 4100K). All macroalgae had equally access to the light and remained in the tank less than five days before their productivity values (i.e. NPP, R, and GPP; see methods below) were measured.

**Experimental setup**

Assemblages were created that varied in terms of total abundance (50, 66, 100, 200 and 600 g), richness (1 to 6 species), and evenness (from 0.40-0.6 to 1). All assemblages are detailed in Table 6. In August 2012, three abundance treatments (50, 100, and 600 g total wet weight of macroalgal assemblages) were established, each treatment having seven different assemblages; the differences due to four possible values of richness (1, 2, 4 and 6 species) and two possible values of evenness (high and low with a $J'$ value of ~1 and ~0.5, respectively) (see Table 6 for details). In July 2013, additional measurements were conducted using three richness values (1, 2 and 5 species) and three different abundance values (66, 200 and 600 g) (cf. Table 6). All treatments were replicated three times.

In the July 2013 experiments, all species present in the polyculture assemblages were also used in monoculture assemblages having a similar total abundance. This approach permitted detection of a possible richness effect (later named the effect of overyielding by calculation) through the addition of separate productivity values from monoculture and then comparing these values with those from the polyculture assemblages. Similar assemblage treatments for the August 2012 and July 2013 experiments were analyzed separately as marginal differences in productivity values were observed between years (e.g. NPP: Pseudo-$F_{1;94} = 3.7891$, $p = 0.059$; R: Pseudo-$F_{1;94} = 3.66211$, $p = 0.062$; GPP: Pseudo-$F_{1;94} = 4.1647$, $p = 0.049$)

All assemblages were used to test five different effects: 1- The identity effect among canopy species (*Fucus* spp.); 2- The identity effect among subcanopy species; 3- The richness effect (using high evenness assemblages); 4- The richness effect (using low evenness assemblages); and 5- The evenness effect (using assemblages of equal richness). The effects on productivity values were tested by contrasting paired values from our assemblages (see detailed list of planned contrasts in Table 7).

For the identity effect, canopy species were tested separately from subcanopy species in order to avoid comparing different species between the canopy and subcanopy layers. Similarly, the richness effect (both at high or low evenness) were always tested using at least one canopy species in each assemblage so as to avoid comparing assemblages having canopy species with those lacking canopy species. Care was taken to separate tests for the richness effect between high and low evenness values, as previous work has observed that dominance may dampen richness effects (Sasaki and Lauenroth 2011). Lastly, the evenness effect on productivity values was tested between assemblages having similar richness values.

In order to facilitate the presentation of results within tables and figures, we used abbreviations for each assemblage. For example, the monocultures of *Fucus distichus edentatus* and *Fucus vesiculosus* were named FUED and FUVE, respectively. Another example is the two-species polyculture having a similar abundance being named "2spJ'high" while a six-species polyculture having a dominant abundance structure between the two constituent canopy species was named "6spJ'low" (see details in Table 6).

**Productivity measurements**

Prior to any measurements, each mesh bag containing the macroalgal assemblages was placed outside for 20 minutes of daylight in a small seawater-filled tank (the tank having a similar temperature and salinity to the tank in the laboratory). The order in which assemblage replicates were measured was randomized. After being extracted from the mesh bag containing the macroalgal assemblage, each species was placed into the benthic chamber in a way to mirror that of a natural community, side by side with a small (~10%) overlap among individuals. All

productivity measurements from each assemblage were performed outside during similar weather conditions (sunlight between 800 and 1000 µmol photon / $m^2$, no clouds, and air temperature conditions between 21 and 24 C°) with the benthic chambers as mesocosms (method described in Migné et al. 2002) that monitored changes in $CO_2$ mole fraction (ppm). The benthic chamber is constituted in a 30 x 30 cm base transparent Plexiglas box with a dome, for a total volume of 18.2 L, and connected to a closed-circuit $CO_2$ infrared gas analyzer (LiCOR LI-820, LI-COR Inc., Lincoln, NE, USA). The data were recorded on a data logger (LiCOR LI-1400; LI-COR Inc.) every 15 seconds during a 10 to 20 minute incubation depending on the response lag. Two benthic chambers were used simultaneously. Measurements were carried out with ambient daylight in order to measure net primary productivity (NPP) and in the dark (chambers covered with an opaque polyethylene sheet) in order to measure respiration (R). Gross primary productivity (GPP) was calculated by adding NPP and R.

**Data analyses**

Within each abundance level, the values of the productivity variables (NPP, R, GPP) among treatments of richness, identity and evenness were compared using Euclidian distance through a permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008). Similarly, with each type of assemblage, values of the productivity variables were compared among abundance levels using pairwise tests within PERMANOVA. Due to the restricted number of permutations within the treatments, Monte Carlo *p*-values (named $p_{mc}$) were used (Anderson et al. 2008). While comparing values among our treatments would fit within classical ANOVA, PERMANOVA was used to avoid the usual normality assumptions of ANOVA, that would be difficult to respect due to the limited productivity data (n = 3) from each assemblage. However, it is worth noting that an examination of results produced by both PERMANOVA and ANOVA of our data were found to be identical (see also Fairclough et al. 2008 for a similar approach).

A set of planned contrasts for each tested effect of identity, richness and evenness (cf. Table 7) generated a total of 71 pairwise tests that were conducted using the same methods outlined above for our use of PERMANOVA. The standard meta-analytical effect size, the response ratio *R*, was

used to determine whether there was a significant general trend in the treatment effects (Hedges and Olkin 1985, Gurevitch et al. 2001). The response ratio *R* is a measure of the outcome, or size effect that compares a control group to an experimental one.

The log response ratio (ln*R*) size effect is calculated as:

$$\ln R = \ln\frac{\bar{X}^e}{\bar{X}^c}, \text{ with its variance } v_{\ln R} = \frac{(s^e)^2}{N^e(s^e)^2} + \frac{(s^c)^2}{N^c(s^c)^2} \quad (1)$$

where $\bar{X}^e$, $s^e$, and $N^e$ are the average value, standard error and the number of data in the experimental group, respectively while $\bar{X}^c$, $s^c$, and $N^c$ are the same for the control group (Rosenberg et al. 2000). In all of our contrast pairings, the control group always had either the lower richness for tests of the richness effect or the lower evenness for tests of the evenness effect, relative to the other group being compared. The experimental group, in contrast, always had either the higher richness or the higher evenness values. For instance, in calculating the ln*R* for contrasting L vs. N (see Table 7), we used the assemblage "2spJ'high" and "6spJ'high" as the control and the experimental terms, respectively. For detection of an identity effect among the two canopy species, *Fucus distichus edentatus* and *Fucus vesiculosus* (hereafter named FUED and FUVE correspondingly), the two species were always considered as the control and the experimental, respectively. Evaluation of the identity effect among the subcanopy species was not possible with the ln*R* due to the number of possible combinations determining which can be considered as the control or experimental groups. Tests for the richness effect always included at least one canopy species in the assemblages. Some contrast-pairings used to test for the richness effect through the addition of productivity values (overyielding by calculation) were considered separately.

Mixed model meta-analyses were used and the effect sizes were considered significant if their bootstrapped 95% confidence interval (using 999 iterations) did not bracket zero. The software PRIMER+PERMANOVA 6.1.12 (PRIMER-E Ltd, Plymouth Marine Laboratory, UK) was used for determining the average difference among treatments while MetaWin 2.1 was used to analyse the ln*R* among planned contrasts. A significance level $\alpha = 0.05$ was applied to all statistical tests.

As pairwise contrasts were planned during the design of the experiment, no correction of $\alpha$ was applied where data were used within more than one comparison.

## Results

### Abundance effect

Macroalgal abundance in biomass had a positive influence on all productivity values (i.e. NPP, R and GPP). *Fucus distichus edentatus* (FUED), showed significant Spearman's $\rho$ correlations of -0.6830, 0.9281 and -0.9220 for NPP, R and GPP, respectively, with increasing abundance (50, 100, 200, and 600 g). Spearman's $\rho$ correlations of -0.9067, 0.9459 and -0.9403 for NPP, R and GPP, respectively, were observed for *F. vesiculosus* (FUVE). When productivity values were reported per gram of macroalgae, they showed similar values up to the 200 g abundance level while (respiration excepted) having slightly lower values at the 600 g level (cf. Fig. 13).

### Diversity profile effects on productivity

Table 8 presents a summary of the results from all pairwise contrasts per tested effects and provides an indication of the number of significant effects out of the total number possible. As a low proportion or no significant results for a given effect tested cannot be interpreted without error (see vote-counting in Hedges and Olkin 1980) formal log response ratio size-effects were assessed on the results and are presented in the following sections.

### Identity effect

No differences were observed in average NPP, R and GPP values for the monospecific assemblages of FUED and FUVE within each abundance level (Fig. 13). However, results from the meta-analysis showed that the monospecific assemblage of FUED had a significantly higher value of NPP, GPP and R than FUVE (Fig. 14).

There were some differences in productivity values among the subcanopy species and within canopy species. Within the 66 g abundance level, Ulvaceae spp. had greater NPP, R, and GPP values than *Porphyra* spp. as well as greater NPP and GPP values than *Chordaria flagelliformis*

(Fig. 13B,H,N). At the 200 g level, all subcanopy algae showed similar NPP values, whereas respiration values were higher for *C. flagelliformis* in comparison with the two other species (Fig. 13 D,J). *Porphyra* spp. had significantly lower GPP values than *C. flagelliformis* but showed no difference with Ulvaceae spp. (Fig. 13P). Ulvaceae spp. showed lower NPP, R and GPP values than FUED (Fig. 13 D,J,P). *Porphyra* spp. had lower NPP values than both canopy species. Finally, *C. flagelliformis* had lower NPP and GPP, but higher R values than FUED.

**Richness effect**

No richness effect was observed within our lowest 50 g abundance level. At 100 g, the polyculture assemblage "6spJ'high" had a greater NPP than the monoculture FUVE (Fig. 13C). Also, "2spJ'high" presented greater NPP values than the "6spJ'high" assemblage (Fig 13C). This example was the single case of negative richness within our results. At the 600 g abundance level, a richness effect was observed with the "2spJ'high" assemblage (i.e. FUED with FUVE) showing greater NPP (2012; Fig. 13E) and GPP (2013; Fig. 13R) values than FUED. Similarly, FUED at 600 g had lower NPP, R and GPP than the five-species assemblage and lower GPP values compared to the "2spJ'high" assemblage (Fig 13 F,I,R).

The log response ratio ($\ln R$) size effect showed a significant positive richness effect for all productivity variables when high evenness was observed within the assemblage (Table 9 and Fig. 14). In the dominance situation (i.e. low evenness), the richness effect became non-significant for NPP and GPP and R became negatively influenced by richer assemblages with a $\ln R$ lower than zero (Fig. 14). The magnitude of the size effect within the richness effect was not linked to the richness difference between the "control" and the "experimental" contrast pairings (correlation coefficients $r = 0.13$: $p = 0.5842$; $r = 0.22$: $p = 0.3457$; $r = 0.022$: $p = 0.9262$; for NPP, R and GPP, respectively). In other words, the size effect did not increase as differences in richness increased within the contrast pairings. Also, the observed richness effect (high evenness) was mainly observed at a certain abundance: at 600 g for NPP and R and 100 g and 600 g for GPP.

Richness effects were also investigated by summing productivity measures at the 200 g level of FUED, FUVE, and the subcanopy assemblages and were compared with values from the 600 g of

the five-species assemblage (cf. Fig. 15). Similarly, the sum of each subcanopy species results at the 66 g abundance level and were compared with their 200 g assemblage results (Fig. 15). This provided two additional indirect tests of the richness effect and was referred to as "overyielding by calculation". Using this method, a negative richness effect was only observed for NPP values with the five-species assemblage showing significantly lower NPP values than a sum ("five-species sum") of the five separate corresponding species (Fig. 15A). No richness effects were observed within the subcanopy species.

**Evenness effect**

At the 100 g abundance level, high evenness within the six-species assemblage positively influenced NPP values (Fig. 13C). At 600 g, NPP in the low evenness assemblage showed lower values than the high evenness assemblage (Fig. 13E). Overall, results of the ln$R$ showed that the evenness positively influenced R but not NPP and GPP of the assemblages, independent of richness (Table 9, Fig. 14).

**Discussion**

In this study, macroalgal assemblages having a variety of diversity profiles were compared in order to test the separate effects of richness, evenness, identity and abundance on the productivity variables of net primary productivity (NPP), respiration (R), and gross primary productivity (GPP). Our results showed a positive richness effect on NPP, R, and GPP, but only when evenness among species was high. Indeed, dominance, or low evenness, damped the richness effect for NPP and GPP, and inversed the richness effect on R when compared with an even assemblage. When richness was similar, an increasing evenness had a positive effect on R only. Not surprisingly, the species (identity) of macroalgae in the monocultures affected productivity variables between macroalgal canopy and subcanopy species. Furthermore, increasing the total abundance in both the monoculture and polyculture assemblages increased productivity values, with constant efficiency per gram of algae up to our second highest abundance treatment (200g/0.09 $m^2$).

**Richness and evenness effect**

Overall, our results agree with previous studies that found richness to enhance community productivity (Eriksson et al. 2006a, Power and Cardinale 2009). Evenness has a limiting effect and works through the richness effect. Indeed, we observed that richness always has a positive effect on NPP, R and GPP but only at high evenness. When dominance was present, the richness effects vanished and even produced a negative positive effect on respiration. The mechanism by which dominance dampens the richness effect on productivity was identified as a negative selection effect (Bruno et al. 2006). In our study, *Fucus distichus edentatus*, which was used as dominant species, often showed slightly higher production rates (NPP, R and GPP) but not always significantly greater that other species. Therefore, differences in our observed richness effects with high and low evenness could not be solely due to negative selection.

Assemblages having high evenness values have only promoted respiration in our study. Previous theoretical and empirical works showed that it was evenness that controlled the effect of richness rather than evenness having direct effect among species (Doak et al. 1998, Eriksson et al. 2006b). This effect is not clear in our study. It has also been suggested that any evenness effect depends on the relative importance of complementarity among species and the selection effect that controls the identity of the dominant species (Polley et al. 2003). Nijs and Roy (2000) applied a mathematical model based on plant growth and nutrient acquisition in order to separate the diversity components and understand the influence of each component on productivity. They found that in the presence of a dominant species having strong productive traits, such as *Fucus* spp. in our study, the dominant species will control the productivity and the abundance of the population present in the community, this scenario also being known as the mass ratio hypothesis (Grime 1998). This may partly explain our observation of a reduced evenness effect on primary productivity and an enhanced richness effect when testing for the richness effect using different levels of evenness.

Overyielding (or the richness effect within primary producers) occurs when the aggregate community performs better than the monoculture. This is usually assessed directly by comparing the performance of species mixtures with monocultures (Hector et al. 2002) and indirectly with

the summation of productivity within the monoculture and then by comparison with the polyculture. The observed overyielding effect in our study came from a direct (ln*R* results) comparison while our indirect (cf. overyielding by calculation results) did not show a significant effect. The observed overyielding may be induced by a complementarity effect (Tilman 1997, Duffy et al. 2007) among macroalgae that originates from light use partitioning among species. Green, red and brown algae capture light from different portions of the electromagnetic spectrum due to their specific chlorophyll pigment content (Haxo and Blinks 1950, Lüning and Dring 1985, Häder and Figueroa 1997). In a rich algal community containing algae having different phenotypes and pigments, a greater portion of the light spectrum may be captured resulting in an enhanced response in community productivity. Cerabolini et al. (2010), using the leaf area index as a measure of light interception by the plant community, demonstrated that in a community marked by an elevated evenness and richness, a greater proportion of the canopy was able to intercept the light and maximize use of light and, ultimately, to increase productivity. Potential light partitioning among macroalgae having different pigments would need further investigation.

The richness effect can lead to transgressive overyielding (polycultures perform better than the best monoculture) or non-transgressive overyielding, (polyculture perform better than the monoculture but not better than the most performing species in monoculture Hector et al. 2002, Bracken et al. 2011). In our study, we observed both overyielding types. Using *Fucus distichus edentatus* (FUED) and *Fucus vesiculosus* (FUVE), as the yield species (most productive) to which the polycultures were compared, we did observe non-transgressive (from n = 6 comparisons) and transgressive (from n = 7 comparisons) overyielding for NPP and GPP while only a non-transgressive type for R (detailed results not shown). To our knowledge, no previous studies involving marine systems have observed transgressive overyielding (Stachowicz et al. 2007 supplementary tables, Crowe et al. 2012). In our studied community, the overyielding effect can provide extra production that would benefit organisms at the higher trophic levels. It has been seen that overyielding in the phytoplankton community can enhance secondary production at the consumer level (introducing the term "trophic overyielding"; Striebel et al. 2012)

In most systems, productivity is tightly linked to biomass. However, the shading effect may limit light availability that controls productivity (Eriksson et al. 2006a). We observed slightly lower values per gram of algae at our highest abundance treatment. This suggests that the shading effect may occur naturally along the shore where there is a large biomass of macroalgal assemblages. This effect might slightly mask the influence of richness and evenness on primary productivity and may explain the lack of clear correlations in our results. Work by Miller et al. (2011) described a strong shading effect with values of primary productivity from phytoplankton and under canopy macroalgae being increased by two- and five-fold, respectively, when the kelp canopy was removed relative to an intact kelp forest.

We also observed a greater richness effect (at high evenness) within the greater abundance treatments relative to those having a lower abundance. Indeed, the richness effect was visible only at 600 g (per 0.09 $m^2$) for NPP and R, and at 100 g and 600 g for GPP. Consequently, a complementarity effect among macroalgal species would probably require a minimum abundance to occur, though this effect may not be enough to compensate the shading effect when a large biomass of macroalgae is present.

**Identity effect**

The identity effect results from the presence of differing adaptation strategies and traits within the community that contribute to enhancing the community primary productivity. The identity effect could be suggested from our data by the presence of varying productivity levels being observed between different subcanopy species. Compared to *Chordaria flagelliformis* and *Porphyra* spp., Ulvaceae spp. was the most productive species but shared similar respiration levels with *C. flagelliformis*. A richness effect was not present among the subcanopy species. However, our results generally showed that the addition of one canopy species (i.e. *Fucus* spp.) to the subcanopy assemblage was enough and necessary to produce a richness effect.

**The use of mesocosms and meta-analytic tools**

Field studies comparing the effects of assemblage diversity profiles remain limited in number as it is challenging to control species abundance within plots (e.g. Lemieux and Cusson 2014). The

use of mesocosms with *in situ* conditions, in which the biomass of the constituent species is controlled, is necessary in order to observe the key elements that influence community productivity and to control for the numerous external factors (e.g. epibionts, encrusting algae, mussels, etc.).

Within natural intertidal communities, productivity values are highly variable (Spilmont et al. 2005). Due to this inherent variability, replication of experiments is key, however large numbers of replication plots or mesocosms in the field may not always be possible. Our use of meta-analysis allowed us to precise the outcome of our "vote counting" contrasts presented in Table 4. Even if the number of significant results may seem relatively low, the measured size effect ($\ln R$) may, or may not, become significant as it takes into account cumulative evidence from separate contrasts (see also Cusson et al. 2014). A review of biodiversity and ecosystem functioning would probably also gain from reporting results using meta-analytic tools such as found in Godbold (2012). Moreover, we showed that to produce conclusive results, polycultures should only be compared to monocultures. Using productivity summation does not seem to pull out the richness effect.

Limitations to our interpretation lie within the generalization of the mechanisms. In our study, we only look at the macroalgae at different levels of evenness, but what we observed might change depending on the trophic level being studied. Recent studies have shown that for adjacent trophic levels, mechanisms promoting productivity may change. Diversity has a differing influence within an assemblage of macroalgae, characterized by a growth competition trade-off than, for example, within a community of herbivores marked by a dominant species (Long et al. 2007).

**Concluding remarks**

Richness can be an important factor influencing ecosystem functions such as productivity. We showed that the richness effect within intertidal macroalgal assemblages does exist and may well be mediated by evenness. When controlling for the number of species, evenness had an overall positive effect on respiration but not on NPP and GPP. The richness effect (overyielding) was greater at higher levels of abundance. Our results suggest that high diversity and evenness are

desirable in order to maximize productivity at the community level. Complementarity among species may be the main mechanism responsible for the observed richness effect. To our knowledge, overyielding has not been previously described for species assemblages from a subarctic ecosystem. The type of species present (identity effect) also influenced values of primary productivity. We also highlighted the importance of taking into account each of the components of diversity (abundance, richness, evenness, and identity) within biodiversity and ecosystem functioning studies.

**Acknowledgements**

We thank S. Lavoie, D-A Gauthier, L. Joseph, S. Cimon for their precious help in conducting laboratory measurements. Thanks to Dr. Denis Chabot and Dr. C. McKindsey for providing access to laboratory space and equipment. We also thank Drs. C. Golléty and D. Davoult for fruitful discussions on productivity measurements. This study is part of J. Lemieux's Ph.D. dissertation at UQAC. This project is a contribution to the research program of Québec-Océan. Financial support was provided by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC; Discovery Grants #371464-2009) and FQRNT (Quebec Funds for Research in Nature and Technology, New University Researchers Start-up Program) to M. Cusson.

Table 5 : Details of species identity, richness, evenness and abundance within all assemblages. Each row represents one assemblage. In total, five levels of abundances (gWW) were used: 50 g, 66 g, 100 g, 200 g, and 600 g; six levels of richness (monoculture, 2, 3, 4, 5 and 6 species (sp)) and two levels of evenness (high $J'$ ~1 and low $J'$ ~0.5). Assemblage names: see Figure 12 for precision. The column "code" refers to the contrast pairings identified in Table 2.

| **Total biomass** | **Year** | **Number of species** | **Evenness** | **Assemblage name** | ***Fucus distichus edentatus*** | ***Fucus vesiculosus*** | ***Chordaria flagelliformis*** | **Ulvaceae** | ***Porphyra* spp.** | ***Ceramium rubrum*** | **Code** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **50** | 2012 | 1 | NA | FUED | 50 | | | | | | A |
| **50** | 2012 | 1 | NA | FUVE | | 50 | | | | | B |
| **50** | 2012 | 2 | high | 2spJ'high | 25 | 25 | | | | | C |
| **50** | 2012 | 2 | low | 2spJ'low | 40 | 10 | | | | | D |
| **50** | 2012 | 4 | NA | subcanopy | | | 12.5 | 12.5 | 12.5 | 12.5 | |
| **50** | 2012 | 6 | high | 6spJ'high | 16.66 | 16.66 | 4.16 | 4.16 | 4.16 | 4.16 | E |
| **50** | 2012 | 6 | low | 6spJ'low | 30 | 10 | 2.5 | 2.5 | 2.5 | 2.5 | F |
| **66** | 2013 | 1 | NA | *Chordaria* | | | 66 | | | | G |
| **66** | 2013 | 1 | NA | *Ulvaceae* | | | | 66 | | | H |
| **66** | 2013 | 1 | NA | *Porphyra* | | | | | 66 | | I |
| **100** | 2012 | 1 | NA | FUED | 100 | | | | | | J |
| **100** | 2012 | 1 | NA | FUVE | | 100 | | | | | K |
| **100** | 2012 | 2 | high | 2spJ'high | 50 | 50 | | | | | L |
| **100** | 2012 | 2 | low | 2spJ'low | 80 | 20 | | | | | M |
| **100** | 2012 | 4 | NA | subcanopy | | | 25 | 25 | 25 | 25 | |
| **100** | 2012 | 6 | high | 6spJ'high | 37 | 37 | 6.25 | 6.25 | 6.25 | 6.25 | N |
| **100** | 2012 | 6 | low | 6spJ'low | 50 | 25 | 6.25 | 6.25 | 6.25 | 6.25 | O |
| **200** | 2013 | 1 | NA | FUED | 200 | | | | | | P |
| **200** | 2013 | 1 | NA | FUVE | | 200 | | | | | Q |
| **200** | 2013 | 1 | NA | *Chordaria* | | | 200 | | | | R |
| **200** | 2013 | 1 | NA | *Ulvaceae* | | | | 200 | | | S |
| **200** | 2013 | 1 | NA | *Porphyra* | | | | | 200 | | T |
| **200** | 2013 | 3 | NA | subcanopy | | | 66 | 66 | 66 | | U |
| **600** | 2012/2013 | 1 | NA | FUED | 600 | | | | | | V/X |
| **600** | 2012/2013 | 1 | NA | FUVE | | 600 | | | | | W/Y |
| **600** | 2012/2013 | 2 | high | 2spJ'high | 300 | 300 | | | | | Z/AA |
| **600** | 2012 | 2 | low | 2spJ'low | 500 | 100 | | | | | BB |
| **600** | 2013 | 5 | high | 5sp | 200 | 200 | 66 | 66 | 66 | | CC |

Table 6 : Summary of planned contrasts among treatments by tested effects within each abundance level. Each contrast pairing is identified by the letter codes from the assemblages described in Table 6. For example the contrast pairing of X vs. AA represents the comparison of the 2013 data of average productivity (NPP, R and GPP) values at 600 g between *Fucus distichus edentatus* (FUED) and the assemblage composed by 300 g of FUED and 300 g of *F. vesiculosus* (FUVE). Also, the first (X) and the second (AA) letter codes indicate which assemblage was the "control" and "experimental" group, respectively, used in the estimation of ln*R* (see methods).

| Effect tested | Abundance (gWW) | | | | |
|---|---|---|---|---|---|
| | 50 | 66 | 100 | 200 | 600 |
| **Identity Fucus** | A vs B | | J vs K | P vs Q | V vs W<br>X vs Y |
| **Identity Subcanopy** | | G vs H<br>G vs I<br>H vs I | | R vs S<br>R vs T<br>S vs T | |
| **Richness (high evenness)** | A vs C<br>B vs C<br>A vs E<br>B vs E<br>C vs E | | J vs L<br>J vs N<br>K vs L<br>K vs N<br>L vsN | R vs U<br>S vs U<br>T vs U | V vs Z<br>W vs Z<br>X vs AA<br>X vs CC<br>Y vs AA<br>Y vs CC<br>AA vs CC |
| **Richness (low evenness)** | A vs D<br>A vs F<br>B vs D<br>B vs F<br>D vs F | | J vs M<br>J vs O<br>K vs M<br>K vs O<br>M vs O | | |
| **Evenness** | C vs D<br>E vs F | | L vs M<br>N vs O | | Z vs BB |
| **Overyielding by calculation** | | | | | P+Q+U vs CC<br>G+H+I vs U |

Table 7 : The abundance effect: comparison of average values per gram of algae between the abundance treatments for net primary production (NPP), respiration (R), and gross primary production (GPP). ns = not significant. *($p < 0.05$); **($p < 0.005$). N/A: no comparison possible.

| | Productivity | NPP | NPP | NPP | R | R | R | GPP | GPP | GPP |
|---|---|---|---|---|---|---|---|---|---|---|
| Assemblage | biomass (g) | 100 | 200 | 600 | 100 | 200 | 600 | 100 | 200 | 600 |
| FUED | 50 | ns | ns | * | ns | * | * | Ns | ns | * |
| FUED | 100 | | ns | * | | ns | ns | | ns | * |
| FUED | 200 | | | ** | | | ns | | | ** |
| FUVE | 50 | ns | ns | * | ns | ns | * | Ns | ns | ** |
| FUVE | 100 | | ns | ** | | ns | ns | | ns | * |
| FUVE | 200 | | | ** | | | ns | | | ns |
| 2spJ'high | 50 | ns | N/A | ns | ns | N/A | ns | Ns | N/A | ns |
| 2spJ'high | 100 | | N/A | ** | | N/A | ns | | N/A | ** |
| 2spJ'low | 50 | ns | N/A | ns | ns | N/A | ns | Ns | N/A | * |
| 2spJ'low | 100 | | N/A | * | | N/A | * | | N/A | ** |
| 6spJ'high | 50 | ns | N/A | | ns | N/A | | Ns | N/A | |
| 6spJ'low | 100 | | N/A | | | N/A | | | N/A | |

Table 8 : For each effect tested, the proportion of contrast pairings having significant results relative to the total number of contrast pairings tested, is shown. See the main text for details on how these effects were determined. Significant results from meta-analysis, shown in Fig. 3, are marked with *. The identity effect among subcanopy species and results of the richness effect for summed values (overyielding by calculation) are not included in the meta-analysis. See Table 6 for abbreviations.

| Effect tested | NPP | R | GPP |
|---|---|---|---|
| **Identity *Fucus* spp.** | 0/5* | 0/5* | 0/5 |
| **Identity subcanopy** | 2/6 | 3/6 | 3/6 |
| **[1]Richness (high evenness)** | 5/20* | 4/20* | 2/20* |
| **[2]Richness (low evenness)** | 0/12 | 1/12* | 0/12 |
| **[3]Evenness** | 2/5 | 1/5* | 1/5 |
| **[4]Overyielding by calculation** | 1/2 | 0/2 | 0/2 |

[1]One negative effect and four positive effects out of 20 for NPP. All positive effects for R and GPP.
[2]Richness effect with low evenness: one negative effect for R.
[3]At 600 g NPP was negatively affected by high evenness. All others showed a positive effect of high evenness
[4]Comparison of added values from the 200 g abundance level of FUED, FUVE and subcanopy treatments (coded: P+Q+U, see Table 7) with the five-species assemblage at 600 g (coded: CC). See Fig. 9 for averages.

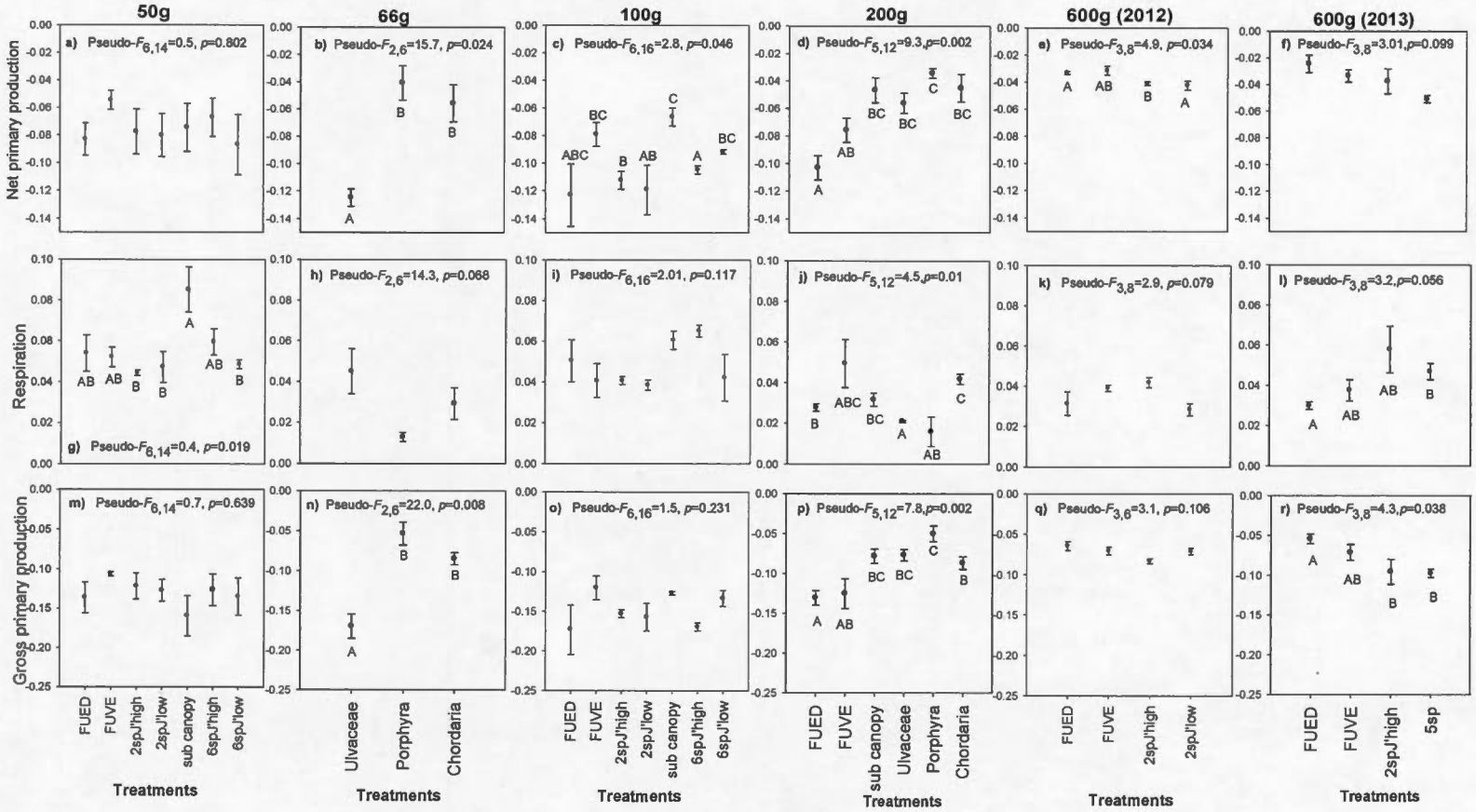


Figure 12 : Average values (±CI 95%) of the productivity variables for net primary production (a to f), respiration (g to i) and gross primary production (m to r) among levels of abundance. All units are mmolCO2*m-2*h-1per gram of wet weight of macroalgae. Unless identified, abundance levels of 50 g and 100 g were estimated in 2012 while levels of 66 g and 200 g were estimated in 2013. See Table 6 for the composition of the assemblage associated with treatment name. Averages (points) having different letters are significantly different ($p < 0.05$).

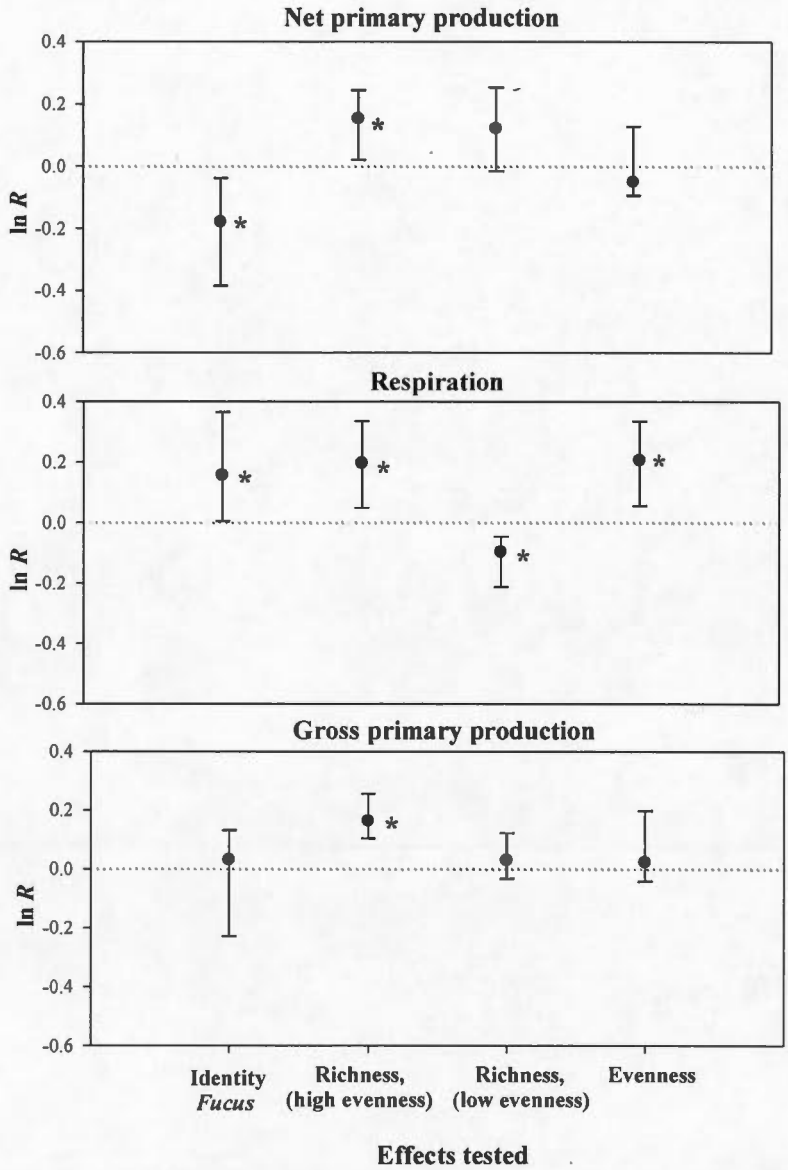


**Figure 13 : :** Log response ratio (ln *R*) of the size effect (with 999 bootstraps, confidence interval 95%) for each effect tested. See Methods and Table 9 for details of all planned contrast pairings that were included in each effect tested. Identity effects for subcanopy species and planned contrasts of richness (overyielding by calculation) are excluded here (see main text for details).

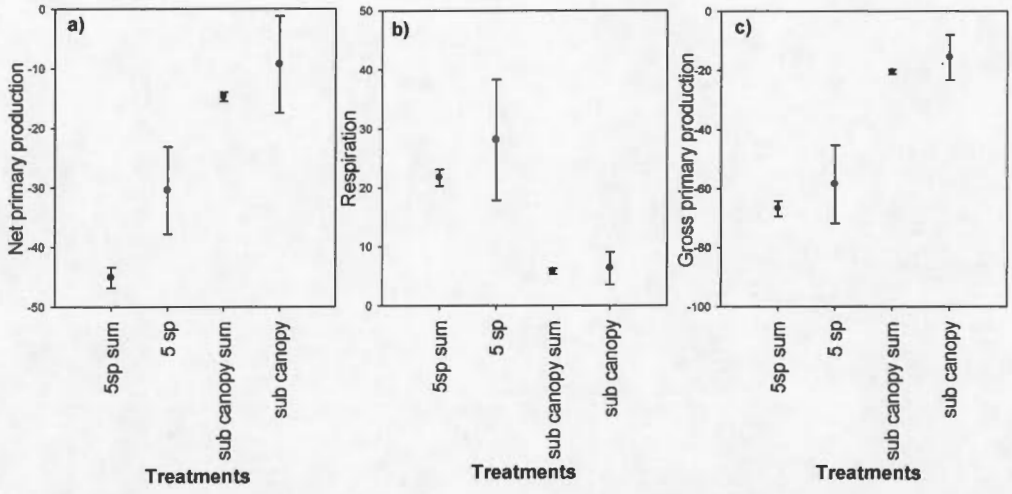


**Figure 14 :** Average values (±CI 95%; all units in mmol $CO_2*m^{-2}*h^{-1}$) for a) NPP, b) R, and c) GPP among treatments from which two new treatments used summation from direct measurements. The values (n = 9) for the "five-species sum" were obtained using the replicate combination of values from three treatments: the two 200 g monoculture FUED and FUVE and the 200 g subcanopy assemblage (in Table 7: treatment codes P, Q, U respectively). The values for the "five-species" correspond to the treatment having the code CC in Table 7. The values (n = 9) for "subcanopy sum" were obtained using the replicate combination of the summation of values from the 66 g treatments of *Chordaria*, Ulvaceae and *Porphyra* spp. (treatment codes G, H, I, respectively). Finally, the values for "subcanopy" correspond to the treatment having the code U in Table 8.

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# CONCLUSION GÉNÉRALE: LIENS ENTRE LES RÉSULTATS DES TROIS VOLETS

## RAPPEL DE LA PROBLÉMATIQUE ET DES HYPOTHÈSES

Les changements climatiques sont au cœur des préoccupations de ce siècle. Les écosystèmes sont modifiés, il y a une perte de la biodiversité importante et un changement dans la composition des espèces. Il y a une nécessité de bien comprendre comment ces bouleversements dans la biodiversité vont affecter le fonctionnement des écosystèmes et les services rendus à l'Homme par ces derniers. Dans cette thèse, j'aborde trois des fonctions importantes de l'écosystème qui sont sujettes à être influencées par un changement dans la biodiversité. La première est la stabilité, car elle apporte une confiance dans les services rendus l'Homme par la biodiversité. La seconde fonction est la facilitation, car elle assure une augmentation de la diversité dans les communautés. La troisième est la productivité primaire ici étudiée en ces trois composantes soit production primaire nette, respiration et production primaire brute, car elle fournit la biomasse à la base de la chaine alimentaire qui soutient le reste de l'écosystème. Ces trois fonctions (stabilité, facilitation et productivité) ont été contrastées avec chacune des composantes de la diversité soit, la richesse, l'équitabilité, l'identité et l'abondance. Les recherches proposées dans ma thèse sont originales, car chaque chapitre, ou volet décrit une fonction des communautés et décortique le rôle de chaque composante de la diversité sur cette fonction. L'objectif commun qui transcende les trois volets est de comprendre comment des changements en richesse, en équitabilité, en abondance et en identité vont influencer le fonctionnement de l'écosystème, ici le fonctionnement des communautés benthiques intertidales. L'hypothèse principale est qu'une augmentation de la richesse, de l'équitabilité et de l'abondance va augmenter la stabilité et la productivité des communautés. Une augmentation de la richesse et de l'équitabilité des espèces fondatrices, responsable de la fonction de facilitation, devrait attirer une diversité d'espèces associées plus élevée. Enfin, l'identité des espèces va influencer les effets de la diversité en contrôlant les traits fonctionnels présents dans la communauté.

Dans les pages suivantes, je fais un résumé des trois volets de ma thèse, qui font ou feront chacun l'objet d'un article qui sera publié dans des revues internationales. Par la suite, je fais le lien entre les volets suivis d'une conclusion générale.

Le volet 1 de la thèse porte sur le lien entre la stabilité des abondances des communautés benthiques intertidales et la richesse et l'équitabilité. Pour ce faire, j'ai suivi sur 2 ans des communautés, 40 quadrats répartis également sur 2 sites. L'effet de richesse et d'équitabilité sur la stabilité des abondances dépend de l'échelle spatiale et temporelle. La richesse a peu ou pas d'impact positif sur la stabilité annuelle des communautés, et ce, à l'échelle locale (sur un site) et régionale (les deux sites combinés). Toutefois sur une période de 2 ans, la richesse a un effet positif sur la stabilité à l'échelle locale et régionale. L'équitabilité a un effet négatif sur la stabilité annuelle des communautés benthiques sur une échelle régionale. Comme le lien entre la diversité et la stabilité des abondances des communautés semble être plus présent sur une échelle de deux ans, il est à croire qu'une série temporelle plus longue pourrait faire ressortir l'influence de la diversité.

J'ai également démontré que la synchronie entre les espèces a un effet négatif sur la stabilité. Lorsque les espèces se mettent à varier de façon identique dans le temps, sans compensation, la stabilité s'en trouve diminuée. Cela pourrait indiquer qu'elles réagissent toutes de la même façon à une perturbation. Dans les communautés à l'étude, la richesse et l'abondance présentent des valeurs en forte diminution au printemps de la seconde année d'étude suivi d'un rétablissement partiel durant la saison chaude. Ceci est dû au raclage par les glaces au printemps. La succession qui s'en suit semble influencer le mécanisme de compensation en contrôlant l'établissement des espèces. De ce fait, la composition (identité) des espèces et le temps de résilience des communautés pourraient masquer un effet potentiel de la richesse et de l'équitabilité. Lorsqu'il y a colonisation d'un milieu les espèces les plus compétitives et avec un taux de reproduction rapide vont coloniser le milieu. Cette première colonisation par des algues éphémères va permettre aux invertébrés de

coloniser à leur trou le substrat en offrant une source de nourriture et une protection contre la dessiccation et chaleur. De plus les algues éphémères peuvent aider les nouvelles pousses de macroalgae à s'établir en diminuant l'intensité des facteurs abiotiques. Des interactions telles que la compensation ne sont pas encore présente, car la se trouve dans une perpétuelle résilience.

En résumé, le volet 1 nous a permis d'établir que l'asynchronie (variation asymétrique des abondances spécifiques dans les assemblages), ou le phénomène de compensation entre les espèces peuvent être des mécanismes importants régissant la stabilité des communautés benthiques. Les effets de la richesse et de l'équitabilité sur la stabilité des abondances varient en fonction de l'échelle à laquelle ces indices sont mesurés (temporelle et spatiale).

Dans le volet 2, j'ai réalisé une expérience *in situ* afin de définir le rôle des composantes de la diversité (richesse, équitabilité, identité, abondance) des trois principales espèces fondatrices du milieu étudié soit *Fucus distichus edentatus, F. vesiculosus* et *Mytilus* spp. sur l'établissement des espèces associées (c.-à-d. espèces ayant colonisées nos parcelles expérimentales) et la production primaire. J'ai observé peu d'effet important des composantes de la diversité des espèces fondatrices sur la richesse, l'identité et l'abondance des espèces associées(Lemieux and Cusson 2014). Toutefois, la structure des espèces associées est différente entre les traitements monospécifiques (1 espèce fondatrice) et les traitements plurispécifiques (trois espèces fondatrices). De plus, cette différence est également perçue à l'intérieur des groupes fonctionnels. Tous les traitements monospécifiques montrent des différences en structure à l'intérieur du groupe fonctionnel des brouteurs et des omnivores lorsqu'ils sont comparés avec les traitements polyspécifiques. On peut supposer que la diversité des HFS influence la présence des espèces en attirant plus d'espèces spécifiques aux HSF présentes dans le milieu. Plus y a HFS plus la structure des espèces associées va représenter cette diversité d'HFS. De plus, la perte ou des changements à l'intérieur des groupes fonctionnels pourraient affecter négativement

les fonctions de l'écosystème en modifiant la performance des processus de l'écosystème que ces groupes offraient.

Les moules possèdent une morphologie distincte et exploitent une niche complètement différente de celle des macroalgues. Les moules modifient le substrat et permet la rétention de sable entre elles attirant des espèces enfouisseurs. Les macroalgues apportent un support et une protection aux organismes tels que des brouteur, on se serait donc attendu a plus de différence entre ces deux espèces fondatrices. Naturellement, ces deux espèces fondatrices montrent des différences importantes dans la structure de leurs espèces associées. Il est intéressant de souligner la similarité entre les espèces associées qui ont colonisé les moules vivantes et leurs coquilles vides. D'après mes résultats, après 16 semaines de recolonisation, les coquilles vides montrent un rôle écologique de facilitation tout aussi important que les moules vivantes en supportant un profil de diversité similaire. Les coquilles vides augmentent l'hétérogénéité du substrat, augmentent, la complexité de l'habitat offrent, des refuges contre la prédation et la dessiccation et permettent au sédiment de s'accumuler entre les valves au même titre que les moules vivantes créant ainsi un habitat favorable à la colonisation. Pour ce qui est des deux espèces de *Fucus* sp. manipulées, il est possible que la redondance dans leur structure soit à l'origine de la forte similarité des communautés d'espèces associées. Sur le terrain, la production primaire de *F. distichus edentatus,* et de *F. vesiculosus* sont semblables. Aussi, la richesse et l'équitabilité de ces communautés (espèces fondatrices et de leurs espèces associées) ne semblent pas avoir affecté la fonction de production primaire. Tout comme au premier volet, seule l'abondance a un effet positif clair sur la productivité primaire. Néanmoins, nos résultats semblent suggérer qu'un niveau d'abondance élevé en nature est critique pour le maintien de la production primaire de la zone benthique.

En résumé le volet 2 indique qu'un changement de richesse et d'équitabilité des espèces fondatrices influence plus subtilement les espèces associées que prévu.

L'identité et la richesse des espèces associées ne changent pas, mais leur structure d'abondance est modifiée en fonction du nombre et de l'équitabilité des espèces structurantes. Ceci pourrait expliquer en partie l'absence de lien fort entre la stabilité et la diversité observée au volet 1.

Dans mes deux premiers volets, en plus de nombreuses observations non publiées, il y avait un manque de réponse claire sur le terrain de l'effet de la richesse et de l'équitabilité sur les valeurs de la production primaire. Comme je n'avais pas de contrôle l'identité des algues et invertébrés et sur la biomasse totale dans les assemblages (et de la proportion en moules, effectuant une forte respiration), j'ai décidé d'évaluer le rôle des macroalgues sur la productivité primaire en milieu contrôlé. Au volet 3, j'ai étudié plus en détail la production primaire des communautés algales. Ici encore, le rôle de la richesse, l'équitabilité, l'identité et l'abondance des espèces sur la production primaire nette (PPN), la respiration (R) et la production primaire brute (PPB) a été étudié. J'ai manipulé en mésocosmes 6 espèces de macroalgues soit *Fucus vesiculosus, F. distichus edentatus, Ulvacea* spp., *Chordaria flagelliformis. Porphyra* spp. et *Ceramium rubrum.*

Des outils méta-analytiques ont été utilisés pour analyser les données renforçant les résultats et les analyses par contrastes conférant à cette section une réelle originalité, car peu travaux utilisent les méta-analyses sur une série de données unique. Les résultats des méta-analyses m'ont fourni un outil précieux dans l'interprétation de plusieurs contrastes testant le même effet (richesse, équitabilité, etc.). Les résultats montrent un effet positif de la richesse sur les trois composantes de la production, mais seulement à équitabilité élevée. Lorsque l'équitabilité est faible, la richesse perd de son importance et seule la respiration est encore affectée positivement. L'équitabilité a uniquement un effet positif sur les valeurs de respiration. Les espèces macroalgales n'ont pas toute la même productivité ce qui engendre un effet clair d'identité. En effet, *F. vesiculosus* à une PPN et R plus faibles que *F. distichus edentatus.* Les espèces de la sous-canopée de nos assemblages sont toutes moins

productives que les espèces de la canopée. *Ulvacea* spp. est l'espèce de sous canopée qui est la plus productive en comparaison de *Chordaria flagelliformis* et *Porphyra* spp. La biomasse totale des assemblages influence positivement la productivité. Toutefois, lorsque l'on reporte les valeurs de productivité des assemblages par gramme, celle-ci se trouve à diminuer à partir de 600g/0.009 $m^2$, probablement dues à un léger effet d'ombrage. C'est-à-dire que plus la biomasse est importante plus la productivité totale est élevée, mais les algues sont proportionnellement moins productives.

Les résultats montrent un effet de surproduction (subséquemment « *overyielding* » ) lorsqu'un assemblage d'algues (polyculture) est plus productif que ses monocultures (chaque algue présente dans l'assemblage mise en monoculture). Plus la richesse augmente, plus l'effet d'« *overyielding* » est important, c'est-à-dire pour cette étude, que les polycultures sont plus productives que les monocultures. La complémentarité entre les algues pourrait être le mécanisme derrière ce phénomène. Comme montré par Bruno et coll. (2005), chaque algue peut aller chercher la lumière dans un spectre qui lui est propre ce qui entraîne une meilleure utilisation du spectre lumineux et donc une productivité de la communauté accrue. D'après nous, cette recherche est la première à avoir démontré un « *transgressive overyielding* » avec des assemblages d'espèces marines c'est-à-dire que, dans certains cas, les polycultures étaient en moyenne plus productives que la plus productive des monocultures.

L'équitabilité, en contrôlant pour la richesse, semble avoir peu d'impact sur la productivité, toutefois elle semble accroître l'effet de richesse. En effet, l'effet positif de richesse sur la production primaire est plus fort à équitabilité élevée qu'à équitabilité faible. Dans un assemblage riche où chaque espèce a les mêmes abondances (forte équitabilité), les traits et les caractéristiques propres à chacune des espèces sont mieux représentées dans la communauté. Comme plus d'individus de chaque espèce participent à la production, les niches écologiques sont d'avantages comblées et les ressources mieux utilisées ce qui permet d'optimiser la productivité

de la communauté. Comme nous sommes en milieu contrôlé, les autres ressources telles que les nutriments ou des associations avec les bactéries ne sont pas présentes dans nos mésocosmes. De ce fait, uniquement la lumière est présente comme ressource partageable. Les algues vont utiliser un spectre de lumière qui leur est propre. En combinant les espèces d'algues, le spectre lumineux va être davantage et mieux capté augmentant ainsi la productivité de l'assemblage d'algues.

En résumé, le volet 3 nous a permis de mieux définir le lien entre la productivité et la richesse qui s'était jusqu'ici faite plutôt discrète dans les 2 premiers volets. En mésocosme, l'impact positif de la diversité (richesse et équitabilité) sur la production primaire nette, respiration et production primaire brute a très bien été démontré. L'équitabilité a aussi un effet positif sur la respiration. La biomasse a un effet positif sur les trois variables de la production.

Tableau 10 : Résumé des principaux résultats des 3 volets. Les symboles + et - démontrent une relation positive (+) ou négative (-) qui a été majoritairement observé dans les résultats.

| | | | Variables | | | |
|---|---|---|---|---|---|---|
| Approche | Fonction | | Richesse * | Équitabilité | Identité | Abondance |
| Expérience naturelle | Stabilité | | + | - | | |
| *In situ* manipulation | Établissement | Diversité | ← | non | → | |
| | | Composition | ← | non | → | |
| | | Structure | oui | oui | oui | oui |
| Mésocosme | Production primaire | | + | + | oui | + |

* Dans l'expérience en milieu naturelle, l'asynchronie entre les espèces semble être responsable pour le lien positif entre la richesse et la stabilité en abondance. Pour les expérience en mésocosme, la complémentarité de l'utilisation du spectre lumineux semble être le mécanisme responsable du lien positif entre la richesse et la productivité.

## LIEN ENTRE LES 3 CHAPITRES

Cette série d'expérimentations en trois volets permet d'avoir des résultats détaillés, obtenus dans plusieurs conditions d'expérimentations, ce qui permet de définir et d'affiner les réponses. Dans le premier volet, j'ai fait une série temporelle de données d'abondance en conditions naturelles dans le but d'obtenir de l'information sur la variabilité naturelle des espèces dans les communautés. Partant de ces observations, dans le volet 2, nous avons manipulé les espèces structurantes directement sur le terrain pour mieux cerner le rôle de la richesse, équitabilité, identité et abondance sur les espèces associées. Finalement, au volet 3, j'ai regardé en mésocosme l'effet de la richesse, l'équitabilité, l'identité et l'abondance des macroalgues sur la production primaire qui avait été jusqu'ici moins bien définie. Ce que j'ai perdu en réalisme dans les conditions naturelles, je l'ai gagné en contrôle. Ce faisant j'ai pu obtenir une meilleure réponse de la relation entre la diversité et la production en éliminant les facteurs environnementaux qui sont très variables sur le terrain et qui peuvent masquer la réponse des assemblages en contrôlant plus finement la biomasse des espèces à l'étude. Les trois volets démontrent que plus nous sommes en milieu contrôlés (biomasse, température, dessiccation...) meilleure est la réponse écologique.

Chaque composante de la diversité (richesse, équitabilité, abondance et identité) a un impact distinct sur les fonctions de la communauté et nous avons démontré l'importance de les traiter séparément. Lorsqu'on étudie qu'une des composantes de la production on ne peut pas obtenir une réponse complète de l'effet de la diversité sur la productivité. En effet, j'ai démontré que les trois composantes de la productivité primaire (production primaire nette, respiration et production primaire brute) réagissent différemment aux composantes de la diversité ce qui pourrait expliquer une partie de la divergence dans la littérature. De plus, j'ai démontré que la durée, l'échelle spatiale et le mode d'expérimentation peuvent générer des résultats différents dans les liens stabilité et biodiversité. Il faut donc considérer ces aspects dans les résultats des futurs travaux recherches.

Pour mes travaux de recherche, le fait d'avoir testé plus ou moins les mêmes hypothèses en milieu naturel, expérimentation en milieu naturel et en mésocosme permet d'obtenir des résultats qui se complètent. Par exemple, lorsque j'ai mesuré la productivité en fonction de la richesse sur le terrain, la réponse était plutôt faible, car elle était masquée par les conditions environnementales. En mésocosmes, le lien entre la diversité et la productivité devient clair. Il est rare de pouvoir expérimenter ces trois approches parallèlement durant mon doctorat. C'est une chance unique de pouvoir développer différentes façon de concevoir des façons de tester les hypothèses pour ensuite faire un lien entre les trois approches expérimentales qui une fois mise ensembles, illustrent bien le fonctionnement de la communauté benthique intertidale du Saint-Laurent.

La zone benthique intertidale est très productive et fournit une grande partie de la biomasse à la base de chaîne alimentaire. Suite à mes travaux de doctorat, si un bouleversement de conditions environnementales causées par les changements climatiques a lieu, je peux affirmer qu'une perte ou un changement dans la biodiversité des organismes benthiques et principalement des macroalgues va avoir un impact négatif sur le fonctionnement des écosystèmes au niveau de la stabilité, de l'établissement des espèces et de la productivité. La suite de ses travaux serait d'étudier la stabilité des abondances sur d'autres sites à proximité et sur une échelle temporelle plus longue. De plus il serait intéressant de regarder l'effet de la diversité des espèces fondatrices le long d'un gradient de stress soit de bas en haut de l'estran. Finalement, les mesures de productivité pourraient être prise sur l'estran tout a long de la saison de croissance, sur plusieurs sites et a plusieurs hauteurs dans la zone intertidale afin d'avoir un patron de variabilité naturelle de la productivité, annuelle, spatiale et le long d'un gradient de stress.

Il est primordial de préserver l'intégrité des zones intertidales afin d'assurer leurs fonctions, et du même coup les produits et services rendus par les écosystèmes marins côtiers. La nature est une valse d'interactions biologiques magnifiquement et

heureusement complexes, qui ne demandent qu'à être écoutées et comprises. Si c'est vrai que le nombre fait la force, la nature l'aura déjà bien comprise et illustrée. Toutes les espèces et compris l'humain sont reliées par un entremêlement d'interactions délicates qui fait que chacun dépends de l'autre pour sa survie. Il y a balancement parfait des liens entre chaque espèce qui permet l'émergence d'une diversité pratiquement infinie et d'une beauté sans égale.

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